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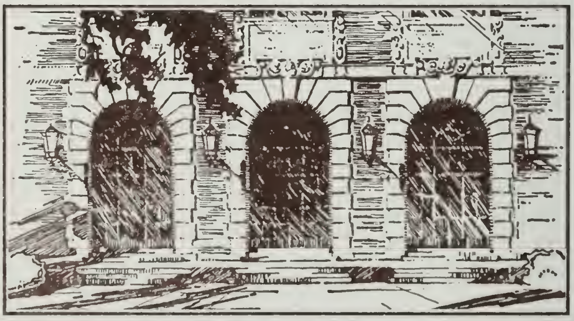

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ANNALS
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VOLUME 44 DECEMBER 20, 1972 ARTICLE 1

HYPORHINA TERTIA, NEW SPECIES (REPTILIA: AMPHISBAENIA), FROM THE EARLY OLIGOCENE (CHADRONIAN) WHITE RIVER FORMATION OF WYOMING

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DAVID S BERMAN
Assistant Curator of Vertebrate Fossils

INTRODUCTION

Beginning with their appearance in the Paleocene (Estes, 1965), amphisbaenids are well represented in the fossil record of most of the Tertiary Period of North America. Over a half-dozen fossil genera are currently recognized, most of which are represented by well-preserved skull material. Fossil amphisbaenids exhibit no remarkable skeletal differences from extant forms and undoubtedly they all shared a common burrowing habit. Their total or partial loss of limbs, acquisition of a worm-shaped body form, compact and strongly ossified skull, and vertically depressed shovel-shaped snout are features commonly pointed to as adaptations to a subterranean habitat.

The position of the amphisbaenids within the Reptilia has been controversial and is still unsettled. A current trend is to regard them as a distinct order, Amphisbaenia, equivalent to the orders Sauria and Serpentes (Gans, 1967; Taylor, 1951). There is less agreement about classification of the amphisbaenids below the ordinal level. In a recent systematic arrangement, Vanzolini (1951) places both Recent and fossil amphisbaenids in a single family, Amphisbaenidae, which includes the four subfamilies Amphisbaeninae, Rhineurinae, Trogonophinae, and Crythiosaurinae. In this grouping, Amphisbaeninae are mainly characterized as having a rounded or laterally compressed snout with laterally placed nostrils, a narrow vertical process of the premaxilla, and pleu-

Submitted for publication April 26, 1971.

rodont dentition. Included in this group is the extant genus *Bipes* from Mexico and possibly southeastern Arizona, whose members are characterized by forelimbs. Members of the subfamily Rhineurinae are distinguished by a strong craniofacial angle, a flattened face and shovel-like snout with a sharp horizontal edge, ventrally placed nostrils, a broad, triangular vertical process of the premaxilla, and pleurodont dentition. Within this group Vanzolini places *Rhineura floridana,* restricted to Florida and representing the only other Recent genus of amphisbaenid found in North America besides *Bipes,* and all the adequately known fossil amphisbaenids of North America. Trogonophinae is distinguished most easily from the two foregoing subfamilies by an acrodont dentition. Vanzolini erected the subfamily Crythiosaurinae, to receive the presumably primitive *Crythiosaurus mongoliensis* Gilmore, 1943, from the Oligocene of Inner Mongolia. It should be noted, however, that Hoffstetter (1962) has cast some doubt on the assignment of *C. mongoliensis* to the Amphisbaenia. He comments that this fossil may more correctly be interpreted, on the basis of Gilmore's figure of the type, as an ophidian. Subdivisions of the amphisbaenids by Taylor (1951) differ somewhat from those proposed by Vanzolini. Taylor recognizes among the Recent and fossil forms the families Amphisbaenidae, Bipedidae, Trogonophidae, Crythiosauridae and Hyporhinidae. In this scheme Bipedidae presumably includes all the forelimbed members, and Trogonophidae those with acrodont teeth. Amphisbaenidae encompasses the remainder of the living amphisbaenids and all the previously known North American fossil forms except the Oligocene genus *Hyporhina,* which is judged worthy of family rank under the name Hyporhinidae Baur, 1893. Crythiosauridae is recognized for the Mongolian genus *Crythiosaurus.* Gans (1960) and Gans and Lynn (1965) have firmly documented the separation of the trogonophids as a distinct family. In a recent check list of the living amphisbaenids Gans (1967) utilizes the two family headings Trogonophidae and Amphisbaenidae (equivalent to the subfamilies Amphisbaeninae and Rhineurinae of Vanzolini), but omits subfamilial divisions. The trogonophids are generally considered the most specialized and the least primitive of the living amphisbaenids (Gans, 1960). The presence of acrodont teeth and absence of the prefontal bone (except in *Trogonophis*) sets this group apart from the remaining living and fossil amphisbaenids, all of which have pleurodont dentition and the prefrontal bone.

When Baur (1893) erected a new family and genus of fossil amphisbaenians, Hyporhinidae and *Hyporhina,* he based his classification on a single specimen: *Hyporhina antiqua* Baur, from the late Oligocene (Whitneyan) White River Formation of Washington County, South Dakota. The specimen was a beautifully preserved skull and lower jaws.

Baur gave only a brief account, however, and it was not until 1928 that a thorough description of *H. antiqua* was given by Gilmore. A second species of this genus, *H. galbreathi,* from the Middle Oligocene (Orellan) White River Formation, Logan County, Colorado, was described by Taylor (1951). At this time Taylor reaffirmed Baur's proposal of the family Hyporhinidae, recognizing as two of the most important diagnostic features: (1) the presence of a postorbital bar formed by a postorbital bone, and (2) the near union of the premaxilla, nasals, and frontals at a single point along the dorsal midline of the skull. Vanzolini, however, assigned *Hyporhina* to the subfamily Rhineurinae.

In the summer of 1965 a field party from Carnegie Museum headed by Drs. Mary Dawson and Craig Black collected a partial skull of an amphisbaenid from the Early Oligocene (Chadronian) White River Formation near Cameron Springs, Fremont County, Wyoming. Its placement in the genus *Hyporhina* is unquestionable and it is described below as a new species.

I am indebted to Miss Helen McGinnis, of Carnegie Museum, who directed my attention to this specimen, and to my wife, Susan, who prepared the illustration.

SYSTEMATICS

Class Reptilia
Order Amphisbaenia
Family Hyporhinidae Baur, 1893
Genus *Hyporhina* Baur, 1893
Hyporhina tertia[1], new species

Figure 1

HOLOTYPE: Carnegie Museum, Section of Vertebrate Fossils, CM 17179, consisting of approximately one half of the anterior part of the skull. This includes almost all the facial portion and about half of the anterior part of the palate. The right mandible is represented by most of the dentary and its dentition.

HORIZON AND LOCALITY: Early Oligocene (Chadronian), White River Formation near Cameron Springs, Fremont County, Wyoming. NW ¼ sec. 1, T. 32N., R. 90W.

DIAGNOSIS: A species more closely resembling *Hyporhina antiqua* than *H. galbreathi.* As in *H. antiqua,* there is an apparent separation of the prefrontal from the border of the orbit in *H. tertia,* though the prefrontal is not as greatly reduced as it is in *H. antiqua. H. tertia* differs from the two previously described species in the sutural pattern between the maxilla, frontal, and prefrontal. In *H. antiqua* and *H. galbreathi* these three bones meet in a Y-shaped sutural contact at the anteriormost point of the prefrontal, whereas in *H. tertia* an ascending process of the maxilla displaces this sutural junction to the mesial border of the prefrontal. In dorsal view, the outline of the snout of *H. tertia* is slightly less blunt, and the relative anteroposterior length of the premaxilla is greater than in either *H. antiqua* or *H. galbreathi.*

---

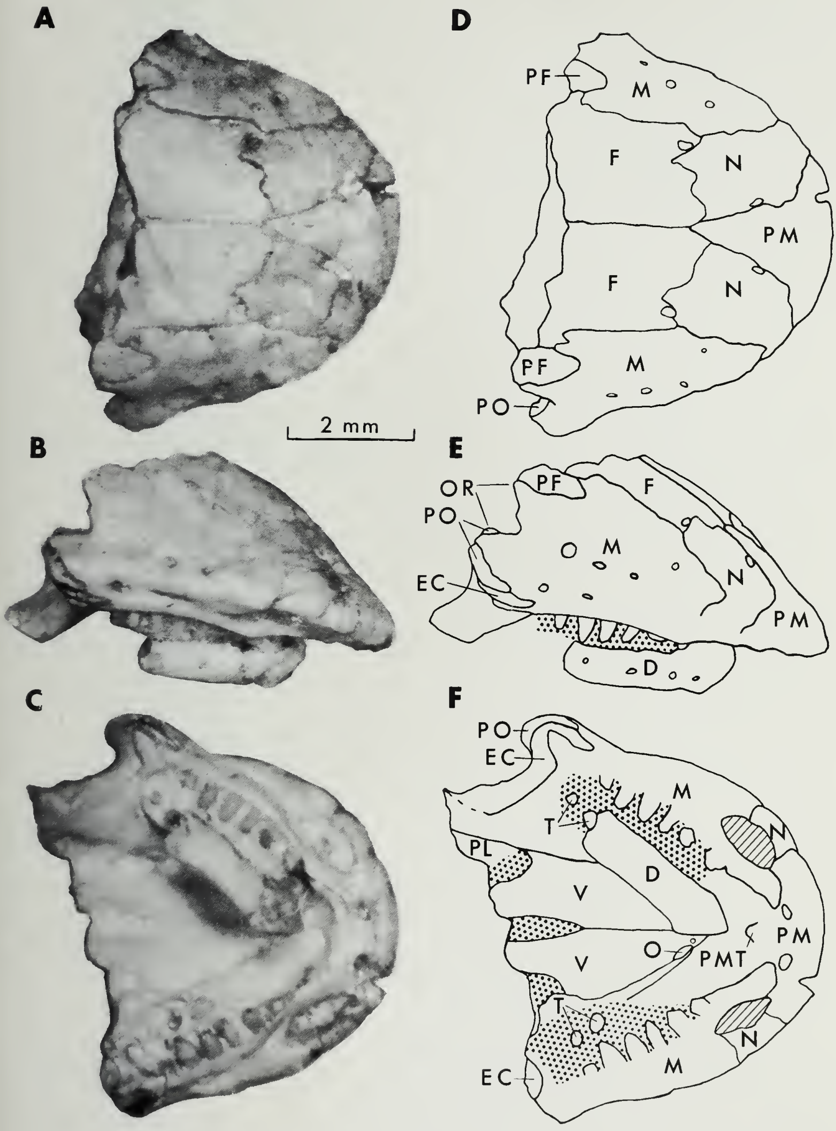
[1] In recognition of this third species of *Hyporhina,* the selection of the specific name is an attempted compromise between numerical and classical taxonomy.

DESCRIPTION: The type of *Hyporhina tertia* (fig. 1) consists of a little less than half of the anterior part of the skull. The total length of the skull was probably about 10 mm. The posterior margin of the skull terminates in a somewhat ragged transverse section, which seen from above, passes from about the anterior border of the left orbit to about the middle of the right orbit. The right side of the skull is consequently more completely represented. The widest point of the skull was probably the distance between the posterior, ventrolateral wings of the maxillae. This dimension is estimated to be about 6.0 mm. in *H. tertia.* The length and width measurements of the types of *H. antiqua* and *H. galbreathi* are 10.0 mm by 5.5 mm (Gilmore, 1928), and 8.5 by 4.4 mm (Taylor, 1951), respectively.

The dorsal view (fig. 1A, D) shows the premaxilla, nasals, frontals, maxillae, prefrontals, and a small portion of the postorbital. The premaxilla is triangular in outline with the width exceeding the length only slightly. Posteriorly it barely wedges between the frontals, narrowly excluding the nasals from medial contact. In the type specimens of *H. antiqua* and *H. galbreathi* the premaxilla is separated from the frontals medially by a narrow contact of the nasals. In a specimen referred to *H. galbreathi* by Taylor (1951), however, a premaxilla-frontal contact is noted. This feature may be variable in this group.

In ventral aspect (fig. 1C, F), the premaxilla has a slightly raised edge that is continuous with the anterior margin of this bone. Just posterior to this ridge, in a broadly concave depression, are two well-marked foramina located near the midline. Immediately posterior to its small contribution to the anteromedial border of the external naris, the premaxilla is sharply waisted by an anterior process from each maxilla, which forms the inner border of the naris. On a line connecting the mid-medial margins of the external nares, the premaxilla makes a sharp step dorsally as it enters the oral cavity. Medially and on the vertical aspect of this step, there is a single, poorly developed tooth that points backward. Both *H. antiqua* and *H. galbreathi* possess a similar, single premaxillary tooth. Behind this and within the oral cavity, the premaxilla sends out two long, widely diverging processes that extend back to about the third maxillary tooth and at a level dorsal to the bases of the maxillary teeth.

Fig. 1. *Hyporhina tertia,* new species. A. dorsal, B. lateral, and C. ventral views of type, CM 17179. D., E., and F. are outline sketches of A., B., and C. Size indicated by 2-mm scale. Stippled areas represent matrix. External nares indicated by oblique ruling. Abbreviations: D, dentary; EC, ectopterygoid; F, frontal; M, maxilla; N, nasal; O, orifice of Jacobson's organ; OR, preserved limits of orbital rim; PL, palatine; PF, prefrontal; PM, premaxilla; PMT, premaxillary tooth; PO, postorbital; T, tips of dentary teeth embedded in matrix; V, vomer.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Dorsally, the premaxilla is flanked by the nasals, except for the tip of the posterior process, which is wedged between the frontals. The nasals narrow and diverge toward the anterior, then widen somewhat before turning back under the rim of the snout to form the anterolateral border of the external nares. There is a well-defined foramen on the border of the nasal, midway along the length of the dorsal, naso-premaxillary suture.

The large frontals are undoubtedly incomplete. Their posterior margins (figs. 1A,D) end in a ragged, broken edge and as much as a third of the frontals may be missing. The remaining portions of the frontals are subrectangular in outline, except at their posterolateral corners, which swing laterally to contact the small prefrontals. In the anterolateral corner of each frontal is a large foramen.

The maxilla is the most extensive element preserved in *H. tertia.* It forms the anterior part of the orbit (figs. 1A,B,D,E), then swings dorsally and posteriorly in the form of a narrow process to contribute to the dorsal border of the orbit. The exact dorsal extent of this process is impossible to determine, and it is very likely that, posterior to the prefrontal, a descending, lateral process of the frontal also contributed to the dorsal margin of the orbit where it made contact with the maxillary process. This would be similar to the condition in *H. antiqua.* A short, posteromedially directed process of the maxilla excludes the anterior third of the medial border of the prefrontal from contact with the frontal. This process is absent in both *H. antiqua* and *H. galbreathi,* where the entire medial border of the prefrontal articulates with the frontal. A row of three to four well-marked foramina runs roughly anteroposteriorly across the mid-lateral surface of the maxilla. Ventral to this series of foramina the external surface of the maxilla makes a sharp ventromedial turn toward the maxillary dentition, forming a smoothly rounded ridge that underhangs the lateral bases of the teeth (figs. 1C,F). Parallel and lateral to this ridge is a broadly concave channel, perforated by a pair of relatively large dental foramina. Medial to the maxillary dentition, there is a wide palatine shelf of the maxilla, notched anteriorly to receive the posterior process of the premaxilla. Posteriorly, the shelf meets the ectopterygoid (preserved most completely on the right side of the palate) in a smooth curve.

The maxilla supports a row of six simple, conical teeth. They are pleurodont or subpleurodont in attachment and inclined posteromedially. The second is larger than the first and third. The third through fifth increase in size to about that of the second, and the sixth and last tooth is much reduced over the fifth. Six pleurodont maxillary teeth are reported in *Hyporhina galbreathi* (Taylor, 1951), whereas in *H. antiqua,* Gilmore (1928:49) reports that the maxilla "carries four small, pointed teeth. . . . that appear to be acrodont in attachment."

The right prefrontal (figs. 1A,B,D,E) is best represented in the type of *H. tertia,* and, although a small portion of this element may be missing posteriorly, it differs noticeably from the prefrontals in the types of *H. antiqua* and *H. galbreathi.* The prefrontal in *H. galbreathi* is unique in being large and forming more than a third of the border of the orbit (Taylor, 1951), rather than being completely separated from the orbit by a process of the maxilla, as in *H. antiqua* and *H. tertia.* In *H. tertia,* the prefrontal is relatively large and is positioned almost directly dorsal to orbit, whereas in *H. antiqua* it is about one third as large, and is located anterior to the orbit.

The postorbital bone (figs. 1B,E) is partially preserved on the right side of the skull. It is seen as a narrow splint of bone, wedged ventrally between the maxilla and a slender external process of the ectopterygoid. The postorbital can be seen ventrally on the lower border of the orbit, where it sends forward a projection that contributes substantially to the ventral border of the orbit. Above this point the postorbital has been broken away. If complete, the postorbital undoubtedly would have continued dorsally as a slender bar enclosing the orbit behind, and uniting with the frontal and parietial above, as reported in *H. antiqua* and *H. galbreathi.* In neither of these forms, however, is there any indication that the postorbital forms any part of the ventral rim of the orbit.

The paired vomers (figs. 1C,F) meet in a straight median suture and occupy a broad triangular space between the palatine shelves formed by the maxillaries and the posterior processes of the premaxilla. The anterior tip of the vomer abuts against the premaxilla for a very short distance laterally, while posteriorly its lateral border appears to insert dorsal to the palatine shelf of the maxilla. At about the level of the posterior maxillary tooth the vomers become constricted and slightly separated as they extend caudally in two narrow tongues. Their posterior extent is not preserved. The incompletely preserved, trough-shaped palatines occupy the area lateral to the posterior processes of the vomers. The narrow depressed area between these processes (now filled with matrix) probably received the parasphenoid. A very faint foramen pierces the vomer near its anterior limit. Immediately posterior to the vomer-premaxillary contact, the lateral margin of the vomer has an oblong notch, closed laterally by the anterior tip of the palatine shelf of the maxilla. This is presumed to be the opening for Jacobson's organ.

The right ectopterygoid is nearly complete. Seen from below, it appears as a band of bone that smoothly arches anteromedially to meet the maxilla. A small, finger-like extension of the maxilla inserts ventrally on the ectopterygoid, giving it an S-shaped pattern. On the external surface of the skull (figs. 1B,E), the ectopterygoid appears as a splint of bone wedged between the ventral border of the postorbital and the maxilla. In comparison, the ectopterygoid in *H. galbreathi* is greatly reduced and does not swing laterally to reach the external surface of the skull (Taylor, 1951). In *H. antiqua* the palatal region is obscured by the closely attached mandibles (Gilmore, 1928). Judging from Gilmore's figures, however, it would appear that the ectopterygoid is not exposed on the external surface of the skull.

The lower jaws are represented by the dentaries only. Little of the left dentary remains, as part was broken away in preparation. The tips of some of the teeth (figs. 1C,F) remain embedded in the matrix left on the palate. The right dentary is about three-fourths complete and is closely applied to the skull. Anteriorly it is complete, and there is a moderately well developed symphysis. The dentary remains relatively uniform in width and depth throughout its length, and when complete held seven teeth. A row of small foramina runs the length of its labial surface. The first five dentary teeth are still intact, though partially hidden by matrix. They are simple conical pegs attached in pleurodont or subpleurodont fashion. All that remains of the last two teeth are the tips of their crowns embedded in matrix on the maxilla. These two teeth would have attached to the missing posterior portion of the dentary. The first and fourth maxillary teeth are nearly equal in size and are much larger than the others. The second and third increase in size posteriorly. The fifth through seventh decrease posteriorly. The lower jaw is not known in *H. galbreathi,* and in *H. antiqua* the number of dentary teeth could not be determined by Gilmore (1928).

DISCUSSION

In 1893, Baur described a new genus and species of fossil amphisbaenid, *Hyporhina antiqua,* from the Late Oligocene (Whitneyan) White River Formation of South Dakota, and proposed the new family Hyporhinidae for its reception. In 1951, Taylor described a second species of this genus, *H. galbreathi,* from the Middle Oligocene (Orellan) White River Formation of Colorado. He agreed with Baur that *Hyporhina* is worthy of family rank. In this report a third species of *Hyporhina* is described, *H. tertia,* from the Early Oligocene (Chadronian) White River Formation of Wyoming. All three species are very similar in general form and are clearly related at the generic level.

The character considered most important by Baur (1893) and Taylor (1951) for the establishment of the family Hyporhinidae was the presence of a postorbital bone. Undescribed fossil amphisbaenids in my possession from the Eocene Bridger Formation of Wyoming and from the Oligocene and Miocene John Day Formation of Oregon have a postorbital bone that closes the orbit from behind in the same manner as in *Hyporhina.* On the family level, these specimens are clearly distinct from *Hyporhina,* and their possession of a postorbital is not a good criterion for establishment of the family Hyporhinidae. Further, there is the likelihood that some of the previously described fossil amphisbaenids may have had a postorbital bone. The postorbital bone is a rather delicate element and there is a tendency for it to be missing in forms known to have it. It is highly probable, therefore, that both postorbitals could be lost through imperfect preservation in a fossil amphisbaenid that has been used as the basis of a new taxon diagnosed as never having this bone.

Although the presence or absence of a postorbital may have little or no taxonomic value, members of the genus *Hyporhina* have a suite of characters that are distinctive enough to warrant separate family ranking. A hyporhinid feature seemingly unique among fossil amphisbaenids is the extremely long, posteriorly directed, paired palatal processes of the premaxilla. In *Hyporhina* these processes share greatly with the maxillae in the formation of a palatine shelf. In other fossil amphisbaenids where this region has been described, the premaxilla is excluded by the maxilla from making any sizeable contribution to the palatine shelf.

The near meeting of premaxilla, nasals, and frontals at a common point on the dorsal surface of the skull is also a character that sets *Hyporhina* apart from all previously described fossil forms. Unique and probably related to this feature is the extreme shortness and bluntness of the facial portion of these shovel-snouted forms.

The three recognized species of *Hyporhina* can be arranged in a morphological series that exhibits a tendency toward a pronounced reduction of the prefrontal bone. The Middle Oligocene *H. galbreathi* would represent the primitive condition, in which the prefrontal is of normal amphisbaenid proportions and forms more than one third of the dorsal border of the orbit. The Early Oligocene *H. tertia* would represent the next stage in this series. Here the prefrontal is slightly reduced and has become separated from the orbit by a dorsal process of the maxilla. And finally, in the Late Oligocene *H. antiqua,* the prefrontal has become reduced to a very small, triangular bone that is located anterior to the orbit and is excluded from the border of the orbit by a process from the frontal above and the maxilla below. This morphological series, though not following exact chronological sequence, suggests that the hyporhinids were well along by Late Oligocene times in what would appear to be an elimination of the prefrontal. Among the present day amphisbaenids, only in the advanced and primarily African trogonophids has there been a loss of the prefrontal.

The unique features of *Hyporhina* listed above are not seen in any other known group of fossil amphisbaenids. This, coupled with a geologic history that spans at least the Oligocene, argues in favor, though on somewhat different morphological grounds than that offered by past workers (Baur, 1893; Taylor, 1951; Vanzolini, 1951), of recognizing this group as part of a distinct lineage deserving of family status. Among the extant forms, I am aware of only one genus, *Monopeltis* (Africa), that closely approaches *Hyporhina* in cranial morphology. In a description of *Monopeltis c. capensis* given by Zangerl (1944), all the key characters noted above for *Hyporhina,* excluding the variable prefrontal bone, are duplicated to some degree. The occurrence of these two groups on widely separated continents is the only major obstacle to suggesting a possible direct relationship. There is neither evidence that the Hyporhinidae survived later than the Oligocene, nor is there any known form that can be seriously considered ancestral to the Hyporhinidae.

REFERENCES CITED

BAUR, G.
1893. The discovery of Miocene amphisbaenians. Amer. Naturalist, 27: 998-999.

ESTES, R.
1965. Note on some Paleocene lizards. Copeia, (1): 104-106.

GANS, C.
1960. Studies on amphisbaenids (Amphisbaenia, Reptilia). 1. A taxonomic revision of the Trogonophinae and a functional interpretation of the amphisbaenid adaptive pattern. Bull. Amer. Mus. Nat. Hist., 119 (3): 129-204.
1967. A check list of recent amphisbaenians (Amphisbaenia, Reptilia). Bull. Amer. Mus. Nat. Hist., 135 (2): 61-105.

GANS, C. and W. G. LYNN
1965. Comments on the thyroid structure of some acrodont amphisbaenids, with remarks on their systematic status. Herpetologica, 21 (1): 23-26.

GILMORE, C. W.
1928. Fossil lizards of North America. Mem. Natl. Acad. Sci., 22 (3): 1-201.
1943. Fossil lizards of Mongolia. Bull. Amer. Mus. Nat. Hist., 81 (4): 361-384.

HOFFSTETTER, R.
1962. Revue des recéntes acquisitions concernant l'histoire et la systématique des Squamates. Colloq. Internat., Prob. Pal., (104): 243-279.

TAYLOR, E. H.
1951. Concerning Oligocene amphisbaenid reptiles. Univ. Kansas Sci. Bull., 34 (1): 521-579.

VANZOLINI, P. E.
1951. A systematic arrangement of the family amphisbaenidae (Sauria). Herpetologica, 7 (3): 113-123.

ZANGERL, R.
1944. Contribution to the osteology of the skull of the Amphisbaenidae. Amer. Midland Naturalist, 33 (3): 764-780.

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VOLUME 44 DECEMBER 20, 1972 ARTICLE 2

THE BOUNDARY BETWEEN *SATYRIUM LIPAROPS* AND ITS SUBSPECIES *STRIGOSUM* (LEPIDOPTERA: LYCAENIDAE)

HARRY K. CLENCH
Associate Curator, Section of Insects and Spiders

The nominate subspecies of *Satyrium liparops* Le Conte, 1833, is so scarce in collections that at one time its very existence was doubted (Michener & dos Passos, 1942). Only a few individuals have been described and discussed in print (Forbes, 1943; Klots & Clench, 1952) since the species was named, well over a century ago.

Mr. Leon Neel, of Thomasville, Georgia, recently presented to Carnegie Museum a fine series of over 40 specimens of *Satyrium liparops* that he collected at various localities in southern Georgia and northwestern Florida. These specimens, along with earlier records and a few additional southeastern specimens, shed new light on nominate *liparops,* especially on its geographical range and intergradation with the more widespread northern subspecies *S. l. strigosum* Harris.

John Abbot, the discoverer of nominate *liparops,* was well acquainted with it, and his manuscript notes, as quoted in Scudder (1872, 1889), bear repeating. He called *liparops* "the Ogeechee brown hair streak butterfly" and considered it to be very rare. Nonetheless he reared it several times and recorded its larval foodplants as holly, a "narrow leaved, jagged, black jack oak" [probably *Quercus catesbyi,* according to Scudder], *Quercus rubra,* and other oaks. He found the duration of the pupal stage to be from 8 to 18 days [Scudder questions the shorter period]. Abbot noted that adults appear early in May, frequent "oak fields and swamps," and that there is only one brood.

Major John E. Le Conte[1] also knew *l. liparops,* either from personal

---

[1] As he spelled it himself (cf. Scudder 1889, frontispiece). In Boisduval & Le Conte (1829-1834) it is invariably spelled "Leconte."

Submitted for publication May 20, 1971.

NATURAL HISTORY SURVEY
JAN 30 1973
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observation or from the notes and paintings of Abbot, it is not clear which.

Boisduval, however, was skeptical. Immediately preceding the original description of *liparops* (Boisduval & Le Conte, 1829-1834 [1833]: 97-98) he inserted a signed *Observation* in which, among other things, he states that *liparops,* as represented by Abbot's painting, "has the greatest resemblance with the *Favonius* of Smith." Farther on he writes, ". . . the so-called new species figured on this plate [31] under the name of *liparops* should be considered the true *Favonius* of Mr. Smith; but because Abbot and my collaborator do not entirely share this view, I have had to yield provisionally to the authority of persons who have made their observations on the spot." The description of *liparops,* on the following page, is credited to Le Conte alone. Boisduval, it appears, declined to accept any responsibility for it!

Despite Boisduval's opinion, and the complete absence of any known specimens, the name *liparops* was not questioned by later authors until 1942, when Michener & dos Passos concluded (independently of Boisduval's remarks, it seems) that it should be made a synonym of *favonius* and the species name *liparops* replaced by *strigosum* Harris.

This synonymy was short-lived. The next year Forbes (1943) published a photograph of a female *l. liparops* from the Okefenokee Swamp in southeastern Georgia. Taken in 1912, this may be the first specimen of nominate *liparops* to have been collected since Abbot's day. Forbes reviewed the situation and concluded that *liparops* should be restored to its previously accepted sense, a conclusion that was entirely justified and has not since been questioned.

From 1943 to the present a few examples of nominate *liparops* have been reported (Klots & Clench, 1952), and in my brief description of the range of *liparops* (Clench, 1961), the statement ". . . southward to northern Florida" was based on the Pellicer Creek specimen listed below.

The type locality of *liparops* is given in the original description simply as "Georgie." Klots (1951) designated Screven Co., Georgia, without explanation, but presumably because Abbot lived there. There is interesting confirmation of this, however, in the common name that Abbot gave to *liparops* (see above). Ogeechee is the name of the river that forms the southwestern boundary of Screven County; it is also the name of a small creek that courses through the middle of the county; and finally, it is the name of a small town, also in the county. We may never know which of the three Abbot had in mind, but he undoubtedly found his *liparops* somewhere in Screven County.

So far as I know, few of Abbot's specimens have survived to the present, and no type of *liparops* is known to exist. One specimen in Carnegie Museum is from 10 miles north of Savannah, only about 35 miles from the presumed type locality, but for two reasons I am unwilling to make a neotype of it: (1) its condition is poor, lacking several actually or potentially useful characters; and (2) the change from *l. liparops* to *l. strigosum* probably occurs near the type locality. The nature of this change is such that 35 miles is by no means close enough for the specimen to be reliably representative.

Nominate *liparops* differs in several ways from the widely distributed, generally more northern, subspecies *strigosum.* The most conspicuous difference is the presence in *l. liparops* of a large patch of fulvous orange on the forewing upperside. This patch occurs in both sexes, but averages a little larger in males. Both tails on the hindwing are longer than in northern *strigosum,* but in *strigosum* from southwestern Georgia and northwestern Florida they are fully as long as in nominate *liparops.* The nominate subspecies averages somewhat larger than northern *strigosum,* but the difference is slight. The orange subterminal crescents on the hindwing underside are somewhat larger in *l. liparops.*

For present purposes I have adopted the development of the fulvous forewing patch as the primary trait separating the two subspecies, but it should be borne in mind that other relevant characters also exist, and some, at least, do not vary in the same geographic pattern.

In order to measure this fulvous patch, I selected six specimens to represent a graded series over the full observed range of its variation, at about equal intervals of development. I scored them numerically from 0 (complete absence of fulvous) to 5 (a large patch of fulvous, from inner margin costad to M_1, and from before middle of wing distad to within about 2 mm of the termen, the whole patch roughly 6 x 7 mm). Using this set of six as a reference scale, each of the studied specimens was assigned a score value. The females figured by Boisduval & Le Conte (1833) and by Forbes (1943) were also evaluated, as were several specimens in the American Museum of Natural History. The results are given below.

LOCALITIES

The following list includes all records (known to me) of any form of *liparops* from the states of Alabama, Georgia, and Florida. Where specimens were available I list the score values. Institutional abbreviations are explained under Acknowledgments.

Alabama

Pike Co.: Spring Hill, l.v (Univ. Michigan), recorded in my notes as *strigosum,* but I have no other information.

Mobile Co.: Mobile, 1926. 1♀, score 0 (AMNH).

Georgia

Fulton Co.: Atlanta (Knudsen, 1955).

Bibb Co.: Macon, 13.v-6.vi (Harris, 1950), reported as *strigosum,* but no other information given; in AMNH 1♂, *leg.* Eustis, no date, score 0.

Screven Co.: (Abbot, *per* Scudder, 1889), the figure of a female in Boisduval & Le Conte, 1833 (pl. 31, fig. 1) has a score of 4.

Chatham Co.: 10 mi N of Savannah, 25.v.1954 (*leg.* J. Bauer, CM), 1♂, score 3.—Savannah (*leg.* H. L. King), ". . . consistently has a large fulvous patch on each forewing" (Klots & Clench, 1952); these specimens in AMNH, 10-20.v.1949/1950, 4♂, scores 2,4,4,4.

Lee Co.: Leland Farms, 13.v.1967 (*leg.* L. Neel, CM), 2♂, scores 0,1; 2♀, scores 0,1.

Dougherty Co.: Albany, 13.v.1967 (*leg.* L. Neel, CM), 1♂, score 0.

Baker Co.: Pineland Plantation, 17.v.1966 (*leg.* L. Neel, CM), 1♂, score 2.

Grady Co.: ½ mi N Hadley Ferry Bridge, 26-28.v.1966 (*leg.* L. Neel, CM), 3♂, scores 1,3,3; 4♀, scores 0,0,1,2.—Sherwood Plantation, 29.iv.1968 (*leg.* L. Neel, CM), 1♂, score 4.

Thomas Co.: Thomasville, 21.v.1969 (*leg.* L. Neel, CM), 1♀, score 0.—Barwick, 21.v.1969 (*leg.* L. Neel, CM), 1♀, score 0.

Echols Co.: Statenville, 18.v.1967 (*leg.* L. Neel, CM), 2♂, scores 5,5; 9♀, scores 2,3,3,4,4,4,4,4,5.

County ? (Charlton, Clinch, or Ware): Honey Island, Okefenokee Swamp, 1.vi.1912 (Forbes, 1943), 1 , score 4.

Florida (See also Postscript)

Escambia Co.: 6.v (Kimball, 1965).

Leon Co.: Tallahassee, 20.v (Kimball, 1965), "impossible to say whether this is typical *liparops* or the form [*sic*] *strigosa*" [I assume, therefore, that it is an intermediate].

Liberty Co.: Telogia, 22,23 v.1965, 22.v.1966, 9.v.1967, 24.v.1969 (*leg.* L. Neel, CM), 8♂, scores 0,1,1,2,2,2,3,4; 7♀, scores 0,0,1,1,1,2,2.—20 mi SSE Telogia, 24.v.1969 (*leg.* L. Neel, CM), 1♂, score 3.

Waukulla Co.: Crawfordville, 11.v.1969 (*leg.* L. Neel, CM), 1♂, score 2.

Flagler Co.: Pellicer Creek, 13 mi N Bunnell, 30.iv.1954 (*leg.* J. Bauer, CM), 1♀, score 5, the southernmost known record of the species.

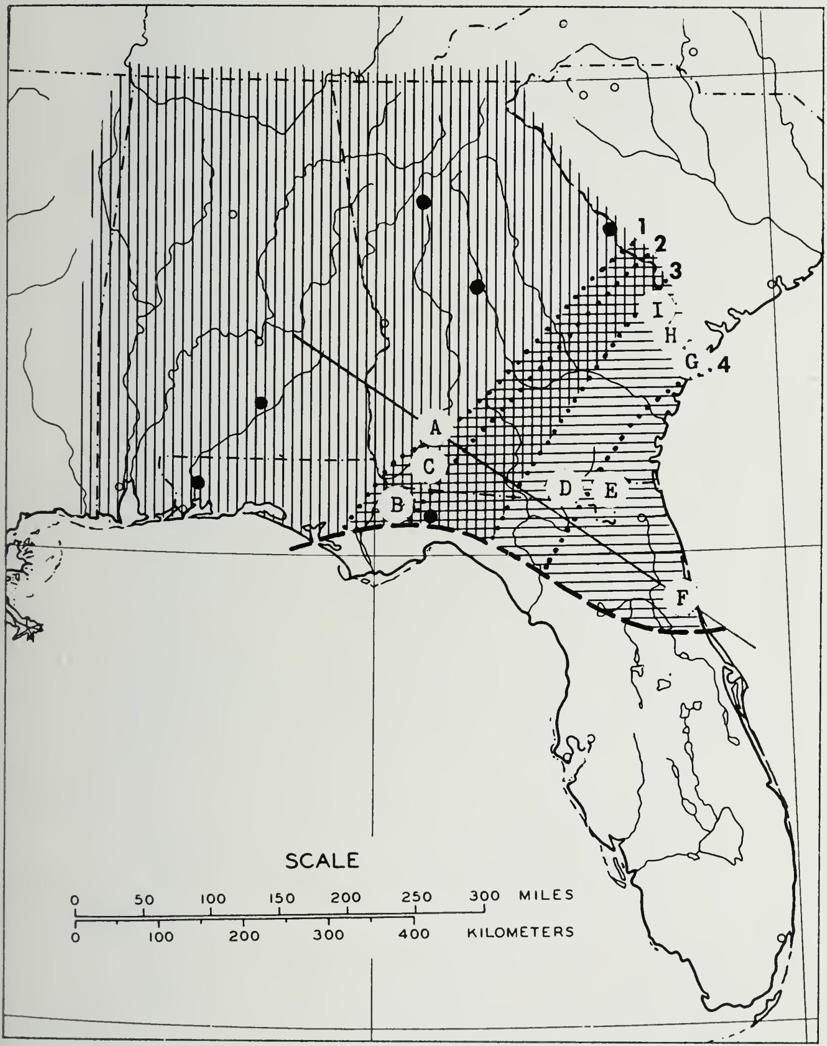
ANALYSIS: The preceding data are enough to provide at least preliminary answers to three questions: What is the range of *l. liparops?* How does it intergrade with *strigosum?* Is there evidence indicating either primary (clinal) or secondary (hybrid) intergradation?

1. *Range:* Given an adequate sample from a locality, the scores may be averaged to give a figure representative of that locality. With enough such localities, suitably disposed, a set of contours could be

Fig. 1. Map of Alabama, Georgia, and Florida showing partial distribution of *Satyrium liparops.* Heavy dashed line marks the approximate known southern limit of the species. Vertical hatching, ssp. *strigosum*; horizontal hatching, ssp. *liparops*; cross-hatching, zone of transition. Large solid dots, literature records, amount of fulvous unknown (but see text). Lettered circles, localities with fulvous known, as follows:

A = Lee + Dougherty cos., Ga., 3♂ 2♀ (av. score 0.4).
B = Liberty + Waukulla cos., Fla., 10♂ 7♀ (av. score 1.6).
C = Baker + Grady + Thomas cos., Ga., 5♂ 6♀ (av. score 1.5).
D = Statenville, Echols Co., Ga., 2♂ 9♀ (av. score 3.9).
E = Honey Island, Okefenokee Swamp, Ga., 1♀ (score 4).
F = Pellicer Creek, Flagler Co., Fla., 1♀ (score 5).
G = Savannah, Chatham Co., Ga., 4♂ (av. score 3.5).
H = 10 mi N Savannah, Chatham Co., Ga., 1♂ (score 3).
I = Screven Co., Ga., 1♀ (score 4).

The solid diagonal line through A and F is the transect (see text and fig. 2).


1
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400
KILOMETERS

drawn showing the spatial change in the degree of fulvous, in effect mapping the range of nominate *liparops* and its transition to *strigosum.*

Satyrium liparops is altogether too rare to expect anything that approaches this ideal in the near future. Mr. Neel's samples, however, are remarkably large for such a scarce species, and they are well disposed. Accordingly I have attempted such a map, even though it has to be approximate rather than precise and definitive. Some of Mr. Neel's locality samples are large enough to be roughly representative in themselves. Others, though small individually, are close enough to each other to be combined into a single average score (e.g., the several stations in Thomas, Grady, and Baker counties, Georgia). In all instances I have had to combine both sexes into the average. The resulting loss of precision is surely small in relation to other uncertainties.

In the map (fig. 1) and in subsequent discussion, I have considered that an average score of less than 1.0 represents *liparops strigosum;* that an average score over 3.0 represents *liparops liparops;* and that an average score between 1.0 and 3.0 represents an intermediate or transitional state. The zone between these values is therefore indicated on the map as the region of transition between the two subspecies.

This map shows that *l. liparops* occupies the southeastern corner of the species range and extends from northeastern Florida northeastward along the coast at least as far as the South Carolina-Georgia line. How much farther it may continue is still unknown for want of material.[2] Although this area is small, the region of transition is smaller still. The change from one subspecies to the other occurs in a narrow band, not much over 60 miles wide.

2. *Transect:* The best samples, as it happens, are grouped rather strategically near a line, crossing and perpendicular to the zone of transition, roughly from Lee and Dougherty counties in Georgia to Pellicer Creek in eastern Florida (see line on map, fig. 1). Plotting the average degree of fulvous development along this line gives the results shown in figure 2. The gradient is obviously steepest at the northwestern (*strigosum*) end, gradually flattening to the southeastward.

3. *Nature of the intergradation:* If a species extends its range in a particular direction and forms subspecies along the way by gradual evolution, the result is called primary intergradation (a cline). Variability of individual populations generally will be comparable throughout, even though the mean value of a variate may change considerably. The change in the mean value along a gradient will often, though not necessarily always, be gradual. If, on the other hand, two subspecies

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[2] Mr. Ronald R. Gatrelle, of Charleston, South Carolina, informs me (*in litt.*, 27 June 1971) that he has taken a single female of *liparops* near Charleston. This specimen has small orange patches on the forewings (score probably 2 or 3, according to his sketch), and thus extends the region of transition between the two subspecies at least as far north as Charleston, about as expected.

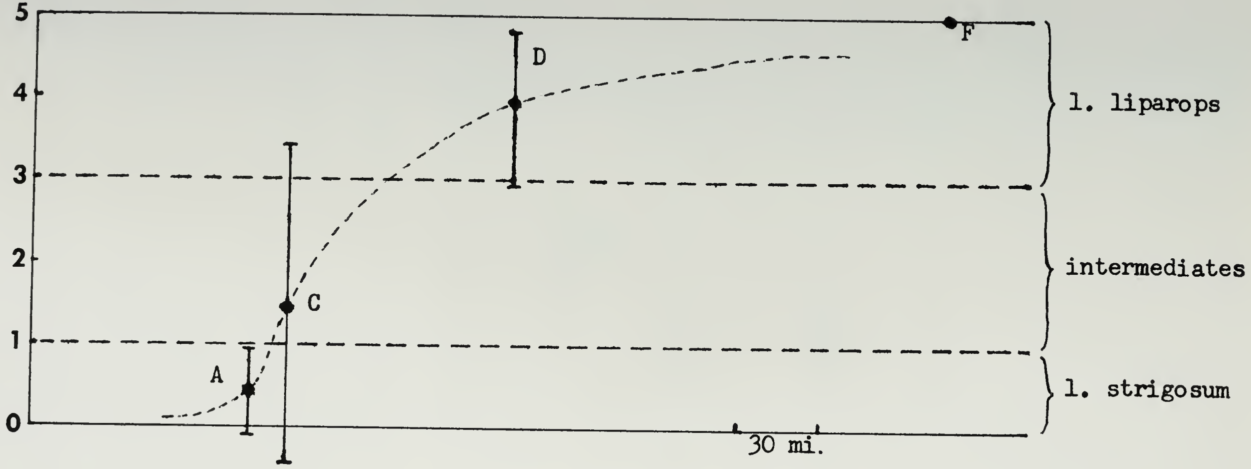

Fig. 2. Transect from localities A to F, showing average amount of fulvous in localities near the line. Letters refer to localities as in fig. 1. Bars represent 1 σ on either side of the mean.

evolved in isolation and subsequent range changes throw the now differentiated forms into contact, then a zone of hybridization or "secondary intergradation" will develop, characterized in part by greater variability of populations within the zone of contact than on either side, and by an abrupt change in the variate mean (sometimes called a "step cline") across the zone.

The character gradient in the transect (fig. 2) shows that the transition from *strigosum* to *l. liparops* is indeed abrupt, occurring over a distance of about 60 miles. The present samples also suggest that variability is greater within the transitional zone than outside it. The four largest samples are represented in histograms (fig. 3) showing the frequency distribution of the amount of fulvous in each. Note that the distribution is more compact in samples outside the zone of transition (A, D; σ = 0.55, 0.92, respectively), and more extended in the two samples from within the zone (B, C; σ = 1.44, 1.43, respectively). The coefficient of variation (V) was calculated for the two largest samples, B (Telogia, Fla.) and D (Statenville, Ga.). The former, from within the zone of transition, has V = 82; the latter, from outside the zone in the area of *l. liparops,* has V = 24: again suggesting increased variability within the zone of transition.

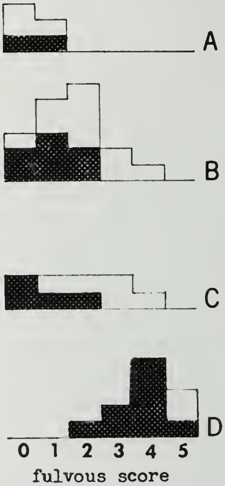

Fig. 3. Histograms showing frequency distribution of amount of fulvous in populations near transect line. Letters refer to localities as in fig. 1. Shaded parts, females; unshaded parts, males.

Thus three different types of evidence—the abrupt change from one subspecies to the other (figs. 1, 2), the form of the histograms (fig. 3), and the coefficients of variation—all agree in indicating that the zone of transition is probably a hybrid zone.

ENVIRONMENT

Mr. Neel has furnished habitat descriptions of most of the localities where he has taken *liparops*. These are given below, together with dates and average scores of the specimens taken.

Leland Farms, Lee Co., Ga. 13.v.1967, 2♂, 2♀. Av. score 0.5, ssp. *strigosum*.

"These specimens were collected on the flowers of Chinese Chestnut (*Castanea* sp.) trees in two groves of these trees separated by a hardwood drain with a creek. The hardwood was mostly oak and gum and has been timbered in the past. The *liparops* all occurred in the first and second lines of trees and never out in the groves. Fire frequency in the hardwood area very infrequent." [L.N.]

Albany, Dougherty Co., Ga. 13.v.1967, 1♂(score 0), ssp. *strigosum*.

"This specimen was collected while [it was] visiting the flowers of Chinese Chestnut. These nut-bearing trees were planted in an old dooryard development immediately adjacent to the hardwood area along the Flint River. This hardwood area in a state of nature began where the open pineland upland stopped and in most areas is semi-swamp (oak, elm, hickory, plus gum and cypress in the low areas) as compared to the mud flat swamps in western Dougherty Co., which contain sweet, black and tupelo gum with oaks, etc. Fire frequency none now but probably burned during extreme drought periods until more or less recently." [L. N.]

Pineland Plantation, Baker Co., Ga. 17.v.1966, 1♂(score 2), intermediate between *liparops* and *strigosum*.

"This specimen was visiting the flowers of New Jersey Tea (*Ceanothus americanus*) growing in open pineland immediately adjacent to the hardwood fringe along the Flint River. Fire frequency where the *Ceanothus* was growing is very regular, but across the fire line in the hardwood area it is very infrequent, probably occurring only during major droughts." [L. N.]

Hadley Ferry Bridge (½ mile north), Ochlocknee River, Grady Co., Ga. 26-28.v.1966, 3♂, 4♀. Av. score 1.4, intermediate population.

"These specimens were all collected while they were visiting the flowers of Chinquapin (*Castanea* sp.), on a sand ridge of about 30 acres that was at one time open pine woods, immediately adjacent to the river swamp of the Ochlocknee River. Poor site, plus indiscriminate timber cutting in the past, has allowed this scrub area to develop with a fire frequency now of about every 5 years. River swamp is burned only during extreme droughts." [L. N.]

Sherwood Plantation, Grady Co., Ga. 29.iv.1968, 1♂ (score 4), probably an intermediate population.

"This butterfly was collected while it visited the flowers of a sparkleberry bush (*Batedendron arboreum* Marsh). The area was open pineland between two creeks with accompanying hardwood forest, the creeks about ¼ mile apart. Fire frequency in the area irregular for the past twenty years (my personal experience), with the average about every third year." [L. N.]

Statenville, Echols Co., Ga. 18.v.1967, 2♂, 9♀. Av. score 3.9, ssp. *liparops*.

"All specimens were collected while they were visiting the flowers of an unidentified shrub growing as part of the understory of a small hardwood drain leading into the Allapaha River. This river at Statenville has a very narrow hardwood fringe, in most areas with the pinelands growing right up to the river banks. Fire frequency at one time was quite regular in the pinelands, but complete fire exclusion has been practiced for the past six to eight years. Hardwood areas only burned during drought periods." [L. N.]

Telogia, Liberty Co., Fla. 22,23.v.1965, 22.v.1966, 9.v.1967, 24.v.1969, 8♂, 7♀. Av. score 1.5, intermediate population.

"The 1965 specimens were collected (along with a fine series of *S. kingi* Klots & Clench) while they visited the flowers of a chinquapin. This tree was located in a roughly two acre patch of woodland between a highway and a railway track. Along the highway on both sides are several very large oak trees and the chinquapin was in a small opening more or less under the large oaks. The remaining area was a patch of slash pine timber. The entire area was obviously at one time a part of a homestead where the owners planted fruit trees, flowers, etc., very extensively. This area has experienced no fire in years and the little slash pine woods have grown up into ty-ty, *Azalea* sp., *Arundinaria* sp. and other shrubs under the slash pine overstory. *Lethe portlandia* occurs here. Out under the large oaks typical scrub is coming in (water oak, Wisteria, plum, etc.). In 1966 we found that the chinquapin had died, but across the highway in the dooryard of the homestead was a fine Chinese Chestnut tree in full bloom. All specimens from that date on were collected on this tree. The site is in the town and is surrounded by small patch farms, dwelling sites, woodlots, etc.: a rural setting." [L. N.]

DISCUSSION

Satyrium liparops reaches its southern limit in northern Florida, the heavy dashed line in fig. 1 indicating its approximate location. The course of this line is based not only on the plotted localities, but on negative evidence from below the line: extensive collecting in peninsular Florida south of Gainesville has never brought *liparops* to light, nor have the considerable efforts of Mr. Neel in western Florida south and west of Tallahassee. Nonetheless, negative evidence being what it is, this line must still be considered quite tentative. Mr. Neel states that apparently suitable environments for *liparops* are found in western Florida at least as far south as the Suwanee River.

The positions of nominate *liparops* and subspecies *strigosum*, the position of the southern species boundary, and the nature and position of the presumptive hybrid zone, all combine to suggest that during the Wisconsin glacial maximum, over 12,000 years ago, nominate *liparops* was displaced far southward, probably occupying southern peninsular Florida, and that it was separated from subspecies *strigosum* by an area (probably in peninsular Florida) in which neither occurred. This possibility is reinforced by the occurrence of a large number of other taxa-pairs that now hybridize in roughly the same area, termed Suture Zone II, and extensively discussed, by Remington (1968).

The land area of Florida alternately grew and shrank on a large scale during the Pleistocene (MacNeil, 1950; Neill, 1957; Zug, 1968). During the glacial periods, when vast amounts of water were impounded in the ice sheets, the shore line was extended seaward of its present location. The increment was slight along the eastern and southern perimeter, but so great along the western coast that the land area of the peninsula was more or less doubled. During the interglacials the sea rose, often well above its present level, and at these times Florida consisted of little more than a small remnant archipelago along the axis of the state, extending southward at the farthest to about the latitude of Lake Okeechobee.

During the Wisconsin glaciation, then, the peninsula was large and available for the suggested southward displacement of ancestral nominate *liparops.* This displacement is also consistent with climatic changes postulated for Georgia, Florida, and the West Indies during Wisconsin time (Neill, 1957; Clench, 1964; Watts, 1970).

A major question is what kept the two *liparops* subspecies apart during the Wisconsin. *S. liparops* is distributed today in a rough continum in the area. There is no obvious physical aspect of the environment that reasonably could be used to explain a Wisconsin-time range disjunction.

In southern Georgia and the adjacent part of Florida, two types of forest are particularly prevalent. One is an open pine forest (mostly Long Leaf and Slash Pine), the other a mixed broadleaf hardwood forest whose principal constituents are beech, Sweetgum, magnolia, hickory, and Spruce Pine. The latter type is climax, but the climax is reached only in areas long protected from fire. Elsewhere the pine forest prevails: fire-tolerant, open, often park-like stands of pine with an understory that may vary from little more than grass and herbs to a fairly dense shrub stratum, depending on the frequency of fires, which are a natural part of this environment (see below).

Satyrium liparops in this area appears to be strongly associated with the interface, or ecotone, between these two forest types. It may be found literally at the boundary, or it may occur in one or the other type, but never far from the boundary. To judge by known occurrences as just described, and by analogy with some other hairstreaks, it is possible that larval feeding and perhaps mating and roosting may occur in the hardwood forest, while adult feeding may take place mostly at the boundary or in the pine forest.

It seems unlikely that *liparops* could occur in either type alone. The hardwood forest would be too shaded, and would probably support too few food flowers for adults. And, as Mr. Neel has observed in numerous samplings, it does not occur in pine forest far from a hardwood area.

Remington (*loc. cit.*) suggests that a moist, dense forest may have been the barrier that divided many of the taxa-pairs he discusses. He points out that several of these taxa-pairs favor semi-wooded, scrubby habitats, and that a moist, dense forest would have been a barrier to them. Such a forest, if of nearly continuous distribution, could have been an effective barrier to *liparops* as well. A forest of this kind must have been located in Florida, probably well southward in the peninsula. Watts (1970) describes the full (Wisconsin) glacial flora in Bartow Co., northwestern Georgia, which is quite similar to a contemporaneous one in eastern North Carolina. This flora consisted of a mixed association of *Pinus banksiana, Picea,* some *Quercus, Carya,* and a large number of other species. The nearest equivalent of this association today is found in northern New England, so the Bartow Co. flora represents a southward displacement of some 700 miles. A corresponding southward displacement of the present range of nominate *liparops* would have eliminated it completely. Assuming, then, that there has been (as there must have been) a certain amount of equatorward compression of life zones, this moist, dense forest probably occurred far southward in Florida, perhaps at about the latitude of Lake Okeechobee.

As was stated above, *liparops* seems to require both the hardwood and the pine forest, and hence could have occupied its present area only when the patchwork forest pattern of today had become established. If the antecedent barrier was a continuous hardwood forest, then the contact of the two subspecies and their consequent hybridization must date from the establishment of the pinelands vegetation in the area.

Remington believes that the pine forest type was probably a product of human disturbance: frequent burning, first by precolonial Indians and then by early European settlers.

For two reasons I doubt that human disturbance has been a significant factor in the origin of this subclimax vegetation type. First, the pinelands communities are fire-adapted (Harper, 1914, esp. p. 184), and the adaptations are many, diverse, and extend to both plant and animal components (Stoddard, 1963). We can only conclude that tolerance to fire was developed long before the arrival of early man in the area—indeed, long before he arrived in the New World. Second, man would by no means have been necessary to set the fires, many of which could have been caused by lightning (Harper, *loc. cit.*; Komarek, 1964). Indians and early settlers assuredly used fire to manipulate their environment, but they were merely perpetuating a long established natural process.

In brief, the fire-conditioned environment had to come in first (cf. Stoddard, 1964). Its arrival may nonetheless have been relatively recent, geologically, spreading in from adjoining areas where, with *liparops,* it had existed earlier; but if we are to find an explanation for its presence in the area, then the explanation must be in some change in climate rather than in human activity.

POSTSCRIPT

In August, 1971, after this manuscript had been completed, I received for study and determination a series of *S. liparops* taken by Mr. R. Kergosien in coastal Mississippi, some 250 miles west of the area from which most of the above samples came. These records are as follows:

Mississippi

Hancock Co.: Fenton, 9.v.1971 (*leg.* R. Kergosien), 2♂, scores 1,1; 1♀, score 0.

Harrison Co.: Big Biloxi Recreation Area [ca. 10 mi N Gulfport], 17.v.1970, 15-30.v. 1971 (*leg.* R. Kergosien), 1♂, score 1; 5♀, scores 0,0,0,0,1.

The average score of this combined lot, 9 specimens in all, is 0.44. While placing the population clearly in *strigosum* as defined above, the fulvous score is unexpectedly high for so far west. It raises the possibility that the western edge of the zone of intergradation may course farther west at its southern end than shown on the map (fig. 1).

All these Mississippi specimens have the long tails and the more extensive orange lunules on the hindwing underside that seem to characterize southernmost *liparops strigosum.*

Florida

Alachua Co.: Gainesville, 19.v.1972 (*leg.* H. Clench, sta. 126), 1♀, score 3.

This single specimen was taken at the edge of a suburban housing development, literally at the interface between an old, possibly virgin, hardwood hammock and a remnant area of a roughly 20-year-old, abandoned Slash Pine plantation, on a Sweetgum leaf about 8 feet above the ground. The habitat conforms perfectly with that postulated above for the species. Although new for the Gainesville area, this record falls within the species range shown on the accompanying map.

ACKNOWLEDGMENTS

I am especially grateful to Mr. Leon Neel, Thomasville, Georgia, for several reasons: first, his presentation to Carnegie Museum (abbreviated CM) of the remarkable series of *Satyrium liparops* on which this paper is principally based; second, his careful notes on the habitats where he has taken *liparops*; third, his discussion of the ecology of *liparops* in correspondence, and his help with several literature references; and last, but by no means least, the hospitality that he and his family extended to my wife and me during a visit in the spring of 1969, which included visits to several of the major environmental types discussed in this paper. I also thank Dr. Frederick H. Rindge, of the American Museum of Natural History (AMNH), New York, for his kind permission to study the *liparops* material there; and Messrs. R. Kergosien and Bryant Mather, of Bay St. Louis and Clinton, Mississippi, respectively, for the opportunity to study the Mississippi material discussed in the postscript.

REFERENCES CITED

BOISDUVAL, [J. A.], AND JOHN E. LE CONTE

1829-1834 [1833]. Histoire générale et iconographie des Lépidoptères et des chenilles de l'Amérique Septentrionale. Paris, Roret, iv + 228 pp., 78 pls.

CLENCH, HARRY K.

1961. Tribe Theclini (pp. 177-220). *In* P. R. and A. H. Ehrlich, How to know the butterflies. Dubuque, Iowa, Brown, [viii] + 262 pp., figs.

1964. A synopsis of the West Indian Lycaenidae, with remarks on their zoogeography. J. Res. Lepid., 2 ("1963"): 247-270, figs.

FORBES, WILLIAM T. M.
1943. What is Thecla liparops? (Lepidoptera: Lycaenidae). Ent. News, 54: 115-117, pl. 1.

HARPER, ROLAND M.
1914. Geography and vegetation of northern Florida. Sixth Ann. Rept. Florida State Geol. Surv.: 163-437.

HARRIS, LUCIEN, Jr.
[1950?]. The butterflies of Georgia, revised. (Georgia Soc. Naturalists), [iii] + vii + 33 pp., mimeographed.

KIMBALL, C. P.
1965. Lepidoptera of Florida (Arthropods of Florida and neighboring land areas, vol. 1). Gainesville (Florida Dept. Agr.), v + 363 pp., 26 pls.

KLOTS, ALEXANDER B.
1951. A field guide to the butterflies (Peterson field guide series). Boston, Houghton Mifflin, xvi + 349 pp., 40 pls.

KLOTS, ALEXANDER B., AND HARRY K. CLENCH
1952. A new species of *Strymon* Huebner from Georgia (Lepidoptera, Lycaenidae). Amer. Mus. Novitates, no. 1600: 19 pp., figs.

KNUDSEN, J. P.
1955. A new host plant record for *Strymon liparops*. Lepid. News, 9: 11-12.

KOMAREK, E. V., Sr.
1964. The natural history of lightning. Proc. Third Ann. Tall Timbers Fire Ecology Conf. (Tall Timbers Res. Sta., Tallahassee, Fla.), 139-183.

MACNEIL, F. STEARNS
1950. Pleistocene shore lines in Florida and Georgia. U. S. Geol. Surv., Prof. Paper 221-F: 95-107, ill.

MICHENER, C. D., AND C. F. DOS PASSOS
1942. Taxonomic observations on some North American *Strymon* with descriptions of new subspecies (Lepidoptera: Lycaenidae). Amer. Mus. Novitates, no. 1210: 7 pp., ill.

NEILL, WILFRED T.
1957. Historical biogeography of present-day Florida. Bull. Florida State Mus., 2: 175-220.

REMINGTON, CHARLES L.
1968. Suture-zones of hybrid interaction between recently joined biotas. *In* T. Dobzhansky, M. K. Hecht, and W. C. Steere, Evolutionary biology, vol. 2, New York, Appleton-Century-Crofts, 321-428, ill.

SCUDDER, SAMUEL H.
1872. Abbott's [*sic*] notes on Georgian butterflies. Canadian Ent., 4: 73-77, 84-87.
1889. The butterflies of the eastern United States and Canada with special reference to New England, vol. 2, Cambridge, Mass. (author), xi, 767-1774.

STODDARD, H. L., SR.
1963. Bird habitat and fire. Proc. Second Ann. Tall Timbers Fire Ecology Conf. (Tall Timbers Res. Sta., Tallahassee, Fla., 163-175.
1964. Opening comments. Proc. Third Ann. Tall Timbers Fire Ecology Conf. (Tall Timbers Res. Sta., Tallahassee, Fla., vii-ix.

WATTS, W. A.
1970. The full-glacial vegetation of northwestern Georgia. Ecology, 51: 17-33, ill.

ZUG, GEORGE R.
1968. Geographical variation in *Rhineura floridana* (Reptilia: Amphisbaenidae). Bull. Florida State Mus., 12: 185-212, ill.

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VOLUME 44 DECEMBER 20, 1972 ARTICLE 3

UPPER DECIDUOUS DENTITION OF THE OLIGOCENE INSECTIVORE *LEPTICTIS (=ICTOPS) ACUTIDENS*

Robert M. West[1]

Introduction

A partial leptictid insectivore maxilla with two deciduous premolars in place was collected by the 1939 Carnegie Museum field party at the early Oligocene Pipestone Springs fossil locality in southwestern Montana. This specimen, CM 9580, assigned to *Leptictis acutidens,* retains the left dP^3, dP^4, and erupting M^2. It permits description of part of the milk dentition of *Leptictis acutidens,* comparison with part of the deciduous dentition of better known *L. haydeni,* and reconstruction of a likely *Leptictis* eruption sequence.

Leptictis acutidens, one of a group of smaller species at present placed in *Leptictis,* was initially described by Douglass in 1902 as *Ictops acutidens,* and was more completely discussed and illustrated by Matthew (1903: 205-207). Van Valen has recently (1967: 235) determined *Ictops* to be a senior synonym of *Leptictis.* He retained the generic name *Leptictis* in order to maintain consistent use of the family name Leptictidae, although this is not required by the International Code of Zoological Nomenclature.

Leptictid deciduous teeth have recently been discussed by several authors. Donald Russell (1964: 47-51, pl. III) described and illustrated dP^4 of the (French Paleocene) questionable leptictid *Adunator lehmani.* Lillegraven (1969: 52-57, figs. 27-28) compared presumed deciduous teeth of Cretaceous *Gypsonictops illuminatus* with those of the Oligocene *Leptictis haydeni.* Clemens (in press) compares *Cimolestes incisus*

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from the Late Cretaceous with the same specimen of *Leptictis haydeni* that Lillegraven used. Although Lillegraven illustrated *L. haydeni,* his discussion concentrated on the Cretaceous leptictids and much description of *Leptictis* was thus omitted.

ABBREVIATIONS

CM—Carnegie Museum, Section of Vertebrate Fossils.

F:AM—Frick collection of American fossil mammals, Department of Vertebrate Paleontology, the American Museum of Natural History.

NMNH—National Museum of Natural History, Smithsonian Institution, Department of Vertebrate Paleontology.

DP^3 AND DP^4 OF *Leptictis acutidens* AND COMPARISON WITH *L. haydeni*

A series of six specimens of *Leptictis haydeni,* each retaining part of the deciduous dentition, has been assembled. These are listed below, and measurements of all their teeth except those of NMNH 16501 are given in Table 1. Only the upper deciduous teeth are described here, as the lower deciduous teeth of *Leptictis acutidens* are not yet known. The lower deciduous teeth of the specimens of *L. haydeni* listed below are similar to those of F:AM 74963, illustrated by Lillegraven (1969).

F:AM 74963—Middle Oligocene, Converse Co., Wyoming.
NMNH 16501—White River Group, Slope Co., North Dakota.
NMNH 167651—Brule Formation, White River Group, Niobrara Co., Wyoming.
NMNH 167652—Brule Formation, White River Group, Niobrara Co., Wyoming.
NMNH 167653—White River Group, Sioux Co., Nebraska.
NMNH 167654—Brule Formation, White River Group, Niobrara Co., Wyoming.

As shown in Table 1, *L. acutidens* is considerably smaller than *L. haydeni,* and some of the differences between the teeth of the two species are allometric, while the more delicate *L. acutidens* differs from *L. haydeni* in several basic morphologic features, as detailed below.

DP^3 of CM 9580 is notable for the large parastyle, actually a separate anterior lobe which significantly extends the labial side of the tooth (Fig. 1). This cusp is more pronounced in *L. acutidens* than in *L. haydeni* (Figs. 2 & 3). The paracone is much larger than the metacone. Both are in a direct line with the parastyle along the labial side of the tooth. The *L. haydeni* metacone is better developed than that of *L. acutidens.* In the latter, the metastyle, a low ridge somewhat longer than in *L. haydeni,* continues the alignment. The protocone is low and lingual to the notch between the paracone and metacone. A low crest extends from the protocone, toward, but without meeting, the metacone

TABLE I

MEASUREMENTS IN MM., DECIDUOUS TEETH OF *Leptictis*

		L. acutidens	*L. haydeni*									
		CM 9580	F:AM 74963		NMNH 167651		NMNH 167652		NMNH 167653		NMNH 167654	
dP^2		Left	Left	Right	Left	Right	Left	Right	Left	Right	Left	Right
	L										3.5	3.4
	W										1.2	1.0
dP^3	L	3.4		4.1	4.9	4.7	4.3	4.2		4.3	4.6	4.6
	W	1.3		3.2	3.2	3.6	2.9	2.9		3.0	3.1	—
dP^4	L	3.0		4.1			4.0	3.7	3.8	4.0	3.8	3.8
	W	2.8		4.2			3.9	3.8	—	4.0	3.9	—
dP$_2$	L											2.8
	W											1.0
dP$_3$	L		3.6		4.7	4.6			3.8	4.0		4.3
	W		1.4		1.8	1.9			2.0	—		—
dP$_4$	L		4.8		4.7	4.6	4.6	4.6	4.5	4.3	4.9	4.8
	Wtr		2.1		2.2	2.3	2.0	2.0	2.8	—	2.2	—
	Wta		2.1		2.5	2.5	2.1	2.2	2.7	—	2.3	—

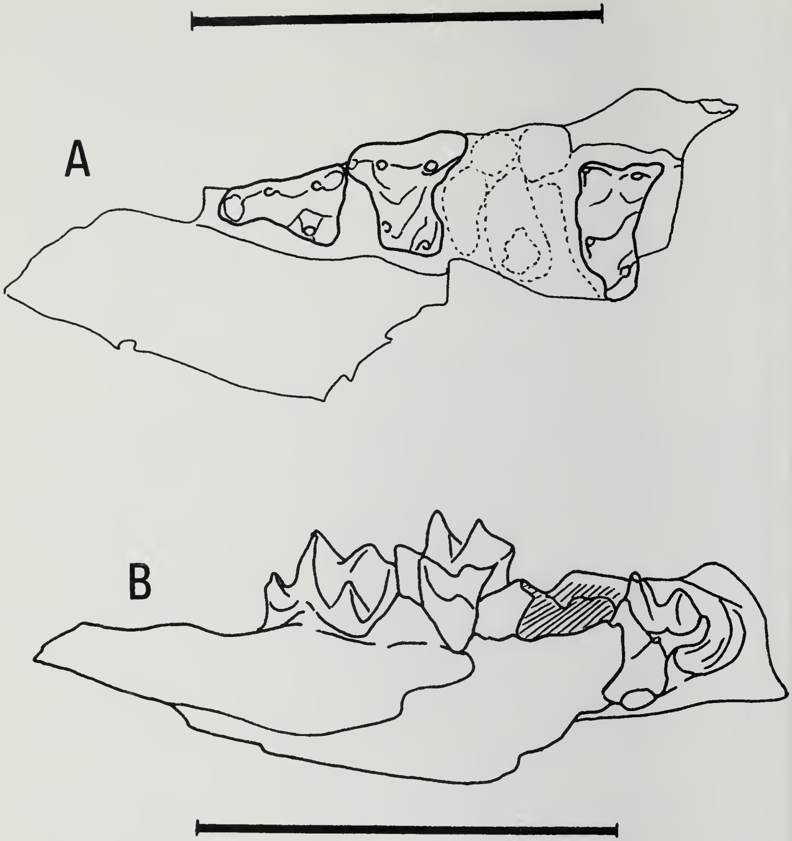


Fig. 1. *Lepticlis acutidens* maxilla, CM 9580. A. Occlusal view. B. Lingual view. Scale indicates 10 mm.

Conules are absent from the dP^3 of *L. acutidens,* but there is a well-developed, isolated paraconule on dP^3 of *L. haydeni.*

A weak cingulum bounds the labial face of the metastyle and metacone, whereas the *L. haydeni* dP^3 has a strong cingulum extending along the entire labial side of the tooth. *L. haydeni* has a small postero-internal platform, not present in dP^3 of *L. acutidens.* As shown in Table 1, dP^3 of *L. acutidens* is relatively narrower than that of *L. haydeni.* The dP^3 length/width ratio of *L. acutidens* is 1: 2.6; that of *L. haydeni* is 1: 1.6. Much of this difference is due to the smaller protocone and absence of conules in *L. acutidens.*

DP^4 in both species is larger and more molariform than dP^3, and is proportionally wider than the molars. The large parastyle is elongate

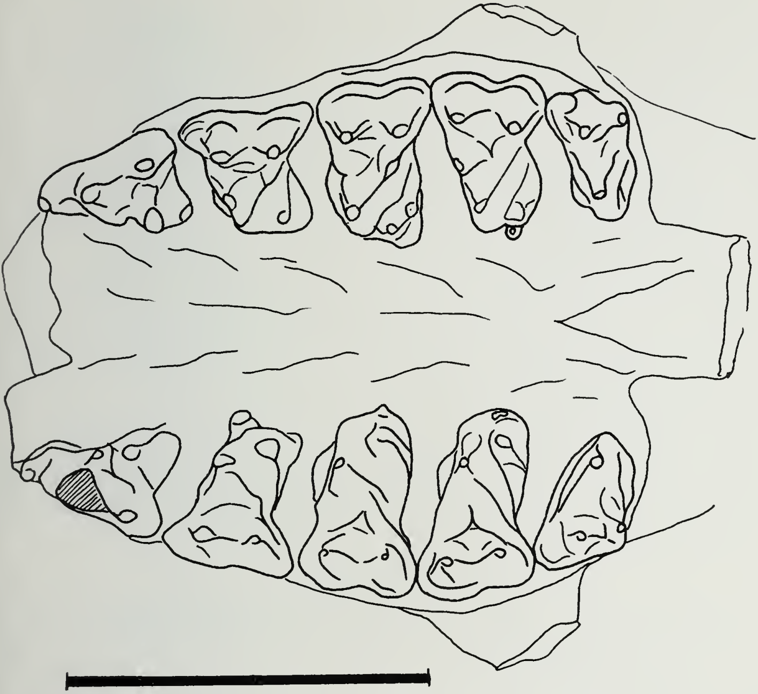


Fig. 2. *Lepticiis haydeni* maxilla, NMNH 167652, occlusal view of upper dentition with dP^3 and dP^4. Scale indicates 10 mm.

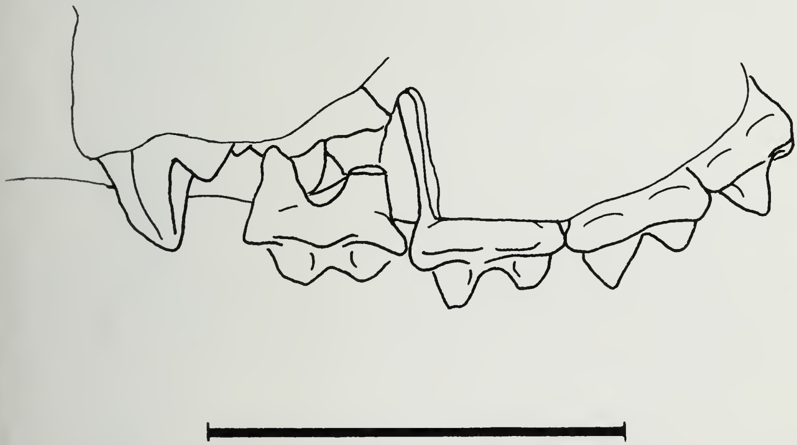


Fig. 3. *Lepticiis haydeni* maxilla, NMNH 167653, labial view of left side showing P^3 and P^4 in place beneath dP^4. A tiny piece of dP^3 remained in the matrix prior to cleaning, and is not shown in the drawing. Scale indicates 10 mm.

linguo-bucally, with a small labial crest in *L. acutidens.* The parastyle does not form a discrete cusp as one dP^3. The paracone of dP^4 in *L. acutidens* is as high as that of dP^3; in *L. haydeni* it is considerably lower. In both species, the dP^4 paracone is joined by a sharp crest to the well-developed, although lower metacone, which is relatively smaller in *L. haydeni.* The unworn protocone of dP^4 of *L. acutidens* is about one-half the height of the labial cones and is located lingual to the protocone. Both species have two conules on dP^4. A deep trigon basin lies in the center of these five cusps. *L. acutidens* has no external cingulum, whereas individuals of *L. haydeni* generally have well-developed external cingula on dP^4. In *L. acutidens,* a broad shelf on the flank of the tooth external to the metacone may be the precursor of a partial labial cingulum. This shelf is not developed in *L. haydeni.* The hypocone is better developed in *L. acutidens,* where it is a definite cusp on the low posterior-internal shelf. The shelf is present in *L. haydeni,* but the hypocone itself is not so discrete. However, an anterior-internal low shelf is present on dP^4 of *L. haydeni,* whereas the anterior part of the *L. acutidens* dP^4 has a smooth face with no indication of cingulum development.

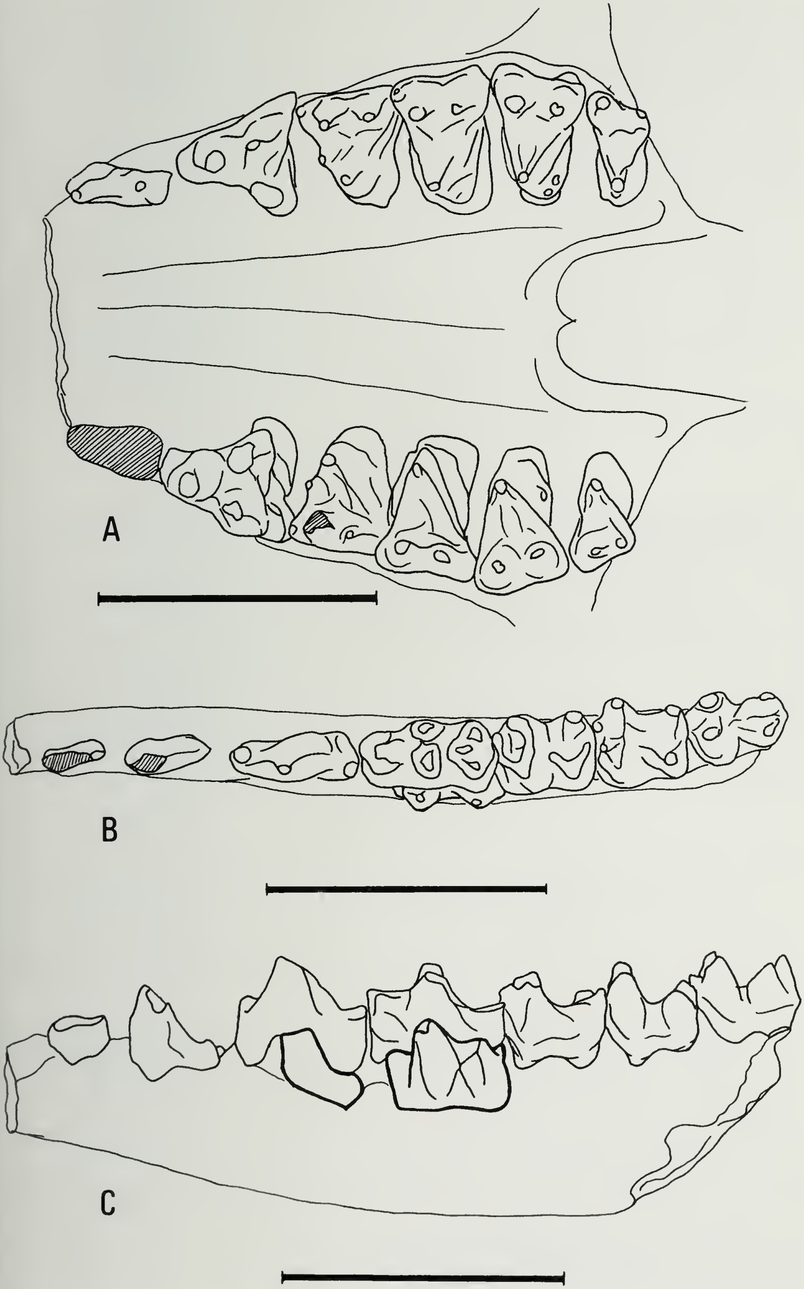
ERUPTION SEQUENCES

Leptictis acutidens: CM 9580 permits speculation only on the final part of the eruption sequence. The permanent first and second molars preceded the appearance of the permanent premolars. The second premolar apparently was in a pre-eruption stage while M^2 was emerging. It cannot be determined from this single specimen whether M^3 emerged before, after, or simultaneously with, P^3 and P^4. Another specimen tentatively assigned to *L. acutidens* (F:AM 74955) shows both P^3 and P^4 in the pre-emergent condition while M^3 is in place and slightly worn. Thus a possible sequence is $dP^{(2,3,4)}$, M^1, M^2, M^3, $P^{(2,3,4)}$, with details within the deciduous and permanent premolar series unavailable.

The wear on the milk premolars of CM 9580 is minimal. This suggests that the permanent molars erupted relatively early in the animal's life, before there could be much wear on the deciduous teeth.

Leptictis haydeni: The six specimens of this species listed above allow a more complete interpretation of the eruption sequence than for *L. acutidens.* The entire molar series is emplaced prior to loss of dP^3 and dP^4, as can be seen on NMNH 167652 (Fig. 2). P_2 is in place in

Fig. 4. *Leptictis haydeni,* NMNH 167651. A. Maxilla, occlusal view showing functional P^4 and remaining dP^3. P^3 is partly visible on the right side. B. Occlusal view of left mandible with both dP_3 and dP_4 in place. P_4 may be seen erupting beneath dP_4. C. Labial view of left mandible with P_3 and P_4 seen erupting beneath dP_3 and dP_4. Scale indicates 10 mm.


A
B
C

NMNH 167653, while both dP_3 and dP_4 are functioning. Presumably the same situation obtained in the upper dentition where the area of the second premolar is missing. P^3 and P^4 became functional almost simultaneously, with dP^4 lost before dP^3 (NMNH 167651, fig. 4).

Thus, the upper eruption sequence is probably $dP^{(2,3,4)}$, M^1, M^2, M^3, P^2, P^4, P^3. Available specimens do not permit suggestions as to the sequence of deciduous teeth eruption, nor as to the presence of a deciduous precursor to the first premolar.

Various specimens of *L. haydeni* show the relatively unworn state of the deciduous teeth at the time of molar emergence, as well as the considerable wear on milk teeth prior to their loss. Granting that the enamel of deciduous teeth shows wear more rapidly than that of permanent teeth, it is still apparent that *Leptictis* maintained a functional row of premolariform dP^3, molariform dP^4 and three true molars for a fairly substantial part of its lifespan.

ACKNOWLEDGMENTS

I wish to acknowledge the gracious hospitality and assistance of Dr. Mary R. Dawson, Section of Vertebrate Fossils, Carnegie Museum, from whom the specimen of *L. acutidens* was borrowed. Dr. Clayton Ray of the National Museum of Natural History lent me the series of *L. haydeni* specimens in his collection. Dr. Malcolm C. McKenna of the American Museum of Natural History offered several valuable suggestions on the draft manuscript. The travel expenses for this study were defrayed by Grant 5532 from the Penrose Fund of the American Philosophical Society. The drawings were prepared by Nelky Seekins.

REFERENCES CITED

CLEMENS, W. A.
In Press. Fossil mammalia of the type Lance Formation. Part III. Eutheria and conclusions. Univ. Calif. Publ. Geol. Sci.

DOUGLASS, E.
1902. Fossil mammalia of the White River beds of Montana. Trans. Amer. Philos. Soc., 20: 237-279.

LILLEGRAVEN, J. A.
1969. Late Cretaceous mammals of the upper part of the Edmonton Formation of Alberta, Canada, and review of the marsupial-placental dichotomy in mammalian evolution. Univ. Kansas Paleo. Contrib., Art. 50 (Vertebrata 12): 1-122.

MATTHEW, W. D.
1903. The fauna of the Titanotherium beds at Pipestone Springs, Montana. Bull. Amer. Mus. Nat. Hist., 19: 197-226.

RUSSELL, D. E.
1964. Les mammifères Paleocènes d'Europe. Mem. Mus. Nat. d'Hist. Nat., series C, XIII: 1-324.

VAN VALEN, L.
1967. New Paleocene insectivores and insectivore classification. Bull. Amer. Mus. Nat. Hist., 135: 217-284.

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VOLUME 44 DECEMBER 20, 1972 ARTICLE 4

CELASTRINA EBENINA, A NEW SPECIES OF LYCAENIDAE (LEPIDOPTERA) FROM THE EASTERN UNITED STATES

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Just over a century ago, in the spring of 1867, William Henry Edwards collected the first known specimens of a curious *Celastrina*. They looked like the common spring form of the Coalburg (West Virginia) area, "violacea"[1], of *Celastrina pseudargiolus pseudargiolus* Boisduval & Le Conte, with which he found them, except that the upper surfaces were black instead of blue-violet.

Edwards (1869*)[2] at first assumed that his specimens were females, but later (1878*) he reported that an examination of the genitalia of several specimens showed them to be males. Still later (June, 1884*) he gave the name "nigra" to what he still believed to be a dimorphic male form of "violacea."

He apparently never realized that there were females corresponding to the males, just as distinctive but not so strikingly different from female "violacea." He had several of these females in his collection, but he simply labeled them as "violacea var. of blue♀," and so far as I can determine he never mentioned them in print.

Strecker (1878*), however, briefly described an "ab. ♀" that may

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[1] Technically this should be called "pseudargiolus," since the species was described from spring individuals. To lessen confusion, however, I here use *pseudargiolus* for the species and nominate subspecies, and "violacea" for the spring form of the latter.

[2] References with dates followed by an asterisk (*) appear only in the synonymy of *ebenina*. Those without the asterisk will be found in "References Cited."

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be the female (which it usually has been assumed to be). He said it was "a form intermediate in colour of upper surface between the blue and brown female [Strecker had not yet seen Edwards's correction of the sex of the dark "form"], neither one nor the other but partaking in a measure of the characteristics of both."

Little has been learned about this strange *Celastrina* since. When referred to at all, it has been called a form of *pseudargiolus.* Forbes (1960*) is the only one to have definitely associated the female (generally called "intermedia" but see below) with the male. For some years I have suspected that this so-called form might be a valid species, but until recently my acquaintance with it was limited almost entirely to museum specimens. In May, 1970, on a trip to southern Ohio, I found a colony of it, and this has prompted me to examine the problem in detail.

The abbreviation CM designates Carnegie Museum.

Celastrina ebenina, new species

Lycaena violacea Edwards (unnamed "♀" form): Edwards 1869, Butterflies of North America 1: [149], pl. [49] fig. 4.

Lycaena violacea (unnamed ♂ form): Edwards 1878, Canad. Ent. 10: 80.

Lycaena lucia Kirby ("ab. a. ♀ Nig." and "ab. b. ♀ Intermedia"): Strecker 1878, Butterflies and Moths of N. Am.: 95 (see below).

Lycaena pseudargiolus Bdv. & Le C., form *violacea,* dimorphic black ♂: Edwards 1883, Papilio 3: 85-97.

Lycaena pseudargiolus, winter form *violacea,* dimorphic ♂ form *nigra* Edwards, June 1884, Butterflies of North America 2: [315], pl. [50] fig. 7; *ibid.* [Dec. 1884-Jan. 1885], Trans. American Ent. Soc. 11: 306.

Cyaniris pseudargiolus violacea [male form] *nigra:* Scudder 1889, Butterflies New England 2: 928, ff.

Lycaena pseudargiolus [form] *violacea,* var. *nigra:* Blatchley 1892, Ann. Rept. Indiana State Geologist 17: 396-397.

Lycaena pseudargiolus form *nigra:* Holland 1898, Butterfly Book: 267, pl. 31 fig. 4 (the specimen illustrated is one of the paratypes of *ebenina:* see below).

Lycaena pseudargiolus var. *nigra:* Skinner 1898, Syn. Cat. N. Amer. Rhop.: 58.

Cyaniris ladon ladon Cramer: Dyar [1903], U. S. Nat. Mus., Bull. 52 ("1902"): 45, no. 440 (name "nig" not mentioned; "intermedia" and "nigra" listed as synonyms).

Cyaniris ladon var. *nigra:* Engel 1908, Ann. Carnegie Mus. 5: 35.

Celastrina argiolus var. *pseudargiolus* ab. *nigra:* Tutt 1908, Nat. Hist. British Lep. 9: 419.

Lycaenopsis pseudargiolus pseudargiolus form ♂ *nigra* and form ♀ *intermedia:* Barnes & McDunnough 1917, Check List Lep. Boreal America: 17.

Cyaniris ladon form *nigra:* Draudt 1921, *in* Seitz, Grossschmett. Erde 5: 818, pl. 144 i (genus and species name corrected 1924, *op. cit.:* 1045, to *Lycaenopsis pseudargiolus).*

Lycaenopsis pseudargiolus pseudargiolus form ♂ *nig* (with *nigra* a syn.) and form ♀ *intermedia:* Barnes & Benjamin 1926, Bull. S. Calif. Acad. Sci. 25: 20 (of reprint), no. 458; McDunnough 1938, Mem. S. Calif. Acad. Sci. 1: 28, no. 475.

Lycaena (Lycaenopsis) pseudargiolus var. *nigra:* Holland 1931, Butterfly Book (rev. ed.): 256, pl. 31 fig. 4.

Cyaniris argiolus pseudargiolus [form ♂] *nigra* and [form ♀] *intermedia:* Clark & Clark 1951, Smithsonian Misc. Coll. 116 (7): 73.

Plebeius argiolus pseudargiolus, "race or rather local variety" *nigra* ("female *intermedia*

Strecker" listed as synonym): Forbes 1960, Cornell Univ. Agr. Exp. Sta., Mem. 371: 126-127.

Lycaena lucia, ab. ♀ *intermedia:* Comstock & Huntington 1960, J. New York Ent. Soc. 68: 236.

Lycaena lucia, ab. ♀ *nig:* Comstock & Huntington 1961, J. New York Ent. Soc. 69: 194.

Lycaena pseudargiolus winter form *violacea* dimorphic ♂ *nigra:* Comstock & Huntington 1961, J. New York Ent. Soc. 69: 194.

Celastrina argiolus pseudargiolus form ♂ *nig* and form ♀ *intermedia:* dos Passos 1964, Lepid. Soc., Mem. 1: 69, no. 481.

Celestrina [sic] *argiolus pseudargiolus (Lycaena nigra):* Brown 1970, Trans. American Ent. Soc. 96: (423), 424, ff., fig. 32.

DISCUSSION OF SYNONYMY

The two names attributed to Strecker ("nig" and "intermedia") are in my opinion *nomina nuda*. Strecker (1878*) never intended them as taxonomic names but simply as Latin descriptives. This is evident because they do not have "nob." [= nobis] after them and because they (and other descriptives in the same work) are not listed in his later catalogue of the type specimens in his collection [Strecker 1872-1900 (1900, Suppl. 3)]. Later uses of these two descriptives as names are either in synonymy (*e.g.*, Dyar [1903]*) or are without description or indication, so the names must be treated as *nomina nuda* and attributed not to Strecker but to whoever first used them as names. If we were to follow the International Code (ICZN 1964), they would become "intermedia" Dyar [1903]* and "nig" Barnes & Benjamin, 1926*. This, however, is dubious practice because both names, when they have been used at all, have been accorded infrasubspecific rank, have no standing under the Code [ICZN 1964: Art. 1 and Art. 45(c)] and are excluded (Art. 1) from its rules.

The name "nigra" is not quite so beclouded: at least Edwards proposed it as a taxonomic name. It was, however, proposed in a clearly infrasubspecific way and has been universally so used ever since. Although this name has no standing under the Code, and therefore technically needs no type specimen, it has been used often enough in the past to have acquired a standing in tradition, and hence a type would be useful. In conjunction with F. Martin Brown's studies of the Edwards types, I selected a lectotype (fig. 1 this article; also Brown, 1970*: fig. 32), a male from the W. H. Edwards collection, labeled in Edwards's hand, "Violacea-/ nigra ♂ / April. Coalb." (Brown, 1970*).

Brown (1970*) uses the combination *"Lycaena nigra"* as a heading, but since he expressly (*ibid.*: 420) includes all North American *Celastrina* under a single species, and lists *"Lycaena nigra"* under *C. argiolus pseudargiolus,* this cannot be taken as an elevation of "nigra" to species status.

In changing the status of this form to full species here, nomenclatorially I have a choice of two courses: I could use the name "nigra" of

Edwards, in which case [ICZN 1964: Art. 10(b)] I would make it available for the first time and it would take the present date and my authorship; or I could propose a new name entirely, since there is currently no available name for the species. I have chosen the second course to avoid the confusion that might result from two identical names with different authors within the same closely related group. In order to reinforce the identity of my name *ebenina* and Edwards's "nigra," however, I am designating the lectotype of "nigra" simultaneously as the holotype of *ebenina.*

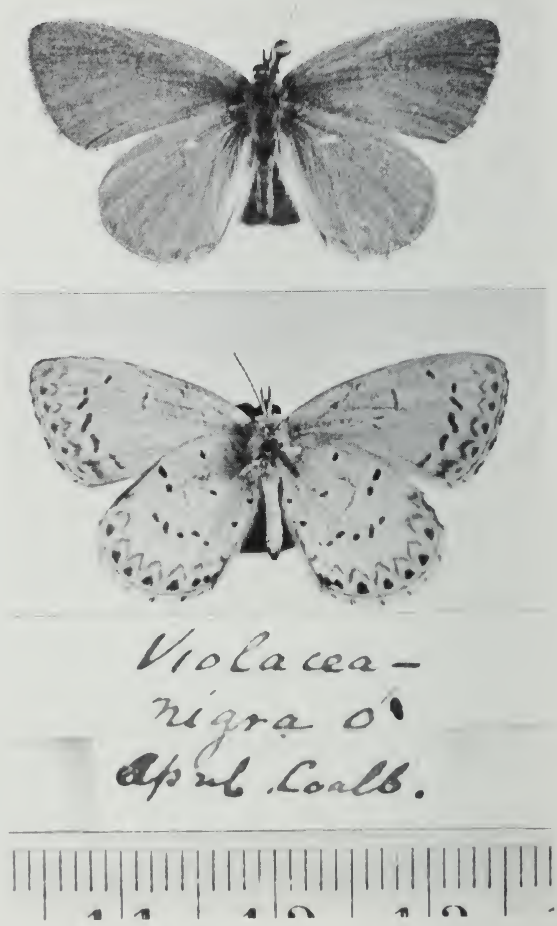


Fig. 1. *Celastrina ebenina,* n. sp., ♂ holotype. This specimen is also the lectotype of the name "nigra" Edwards. Scale at bottom is in millimeters.

DESCRIPTION (figs. 1-5)

MALE UPPERSIDE: uniform blackish brown when fresh, fading to brown in older specimens. Rarely, a few dark blue scales may be present, particularly on the hindwing in some of the areas normally blue in the female. Inner margin of hindwing fuscous to gray. Fringe dingy white, checked with fuscous on vein-ends; the width of the fuscous parts is subequal to the intervening white on the forewing, but much thinner than the white on the hindwing. No androconial scales are present.

FEMALE UPPERSIDE: both wings slightly lustrous pale gray-blue, heavily marked with fuscous as follows: forewing broadly on costa, inward to M_1 and including nearly all the discal cell (all but the posterodistal corner); broadly on termen, covering the outer third of vein M_3; and in base distad to about the origin of Cu_2 or a little before; hindwing broadly on costa, inward to M_1 (but sometimes with a small area of blue in Rs-M_1) and costal cell vein; in base distad to about middle of cell, and (more blackish) along vein 2A from base to near termen, gradually fading inward before reaching Cu_2. Inner margin itself ashy white. A fuscous complex terminal border consists of the following: a fine black terminal line (which does not fade to brown with age); an adterminal series of round or oval fuscous spots separated from the terminal line by a thin line of dull pale blue interrupted by fuscous at the veins; a series of dull pale blue crescents capping the adterminal spots, from M_1 to 2A; and basad of the crescents a crenulate fuscous subterminal band, normally about as thick as the adterminal spots but a little paler. On each wing there is a long, slender, cell-end bar, and all veins crossing the blue are thinly fuscous. Fringe as in the male.

MALE UNDERSIDE: almost exactly as in "violacea" (i.e., the spring brood of *C. p. pseudargiolus*). The pale ashy ground is the same; the fuscous pattern elements are the same in character and disposition except that the adterminal spots are noticeably larger and show no tendency to fade costad, and there is no evidence of the "marginata"-like blurring of the marginal elements sometimes found in "violacea" in varying degrees (and which becomes characteristic of the spring brood of *pseudargiolus lucia* Kirby farther north). In "violacea" the basal and pm spots are often much darker than the marginal pattern elements. This is less often true in *ebenina,* but it does occur.

FEMALE UNDERSIDE: as in the male.

MALE GENITALIA (fig. 10): identical to those of *C. p. pseudargiolus* (fig. 11).

HOLOTYPE: male, Coalburg, Kanawha Co., West Virginia, April, *leg.* W. H. Edwards. This specimen is also the lectotype of *Lycaena pseudargiolus* winter form *violacea,* dimorphic ♂ form *nigra* Edwards, 1884 (see above).

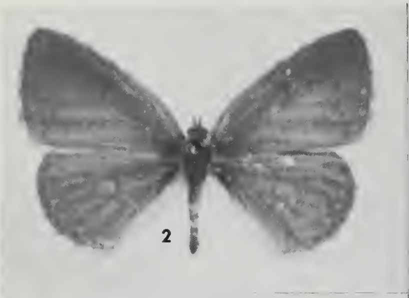
PARATYPES: From the collection of W. H. Edwards: 6♂, labeled "violacea ♂" or "violacea-nigra ♂" and "Coalb." or "Kan^a," bearing various dates in April 1871, 1872, 1879, 1881, 1884 or no date. One of these is illustrated by Holland, 1898*, pl. 31 fig. 4, and another by Holland, 1915, pl. xcii fig. 4; 1♀, labeled "violacea ♀ aberr. March Coalb."

From the collection of T. L. Mead: 13♂, mostly labeled "violacea Brown ♀" and "W Va," dated 17, 23, 27 April 1872; and 5♀, labeled "violacea var. of Blue ♀" and "W Va," dated 24, 26, 27 April 1872.

From the collection of W. J. Holland: 11♂, labeled simply "W. Va." One of these additionally labeled ♂ genitalia slide C-757 [HKC].

All the above paratypes are presumed to have been taken in the vicinity of Coalburg, Kanawha Co., West Virginia.

Holotype, 30 ♂ and 6 ♀ paratypes, CM Ent. type series no. 671.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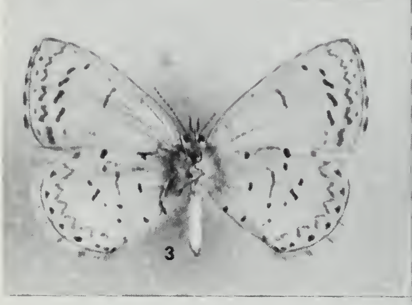
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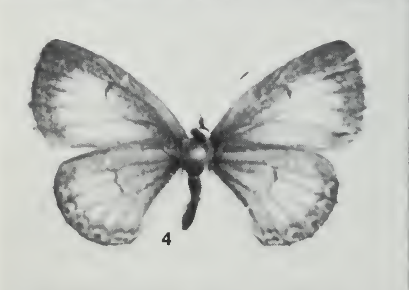
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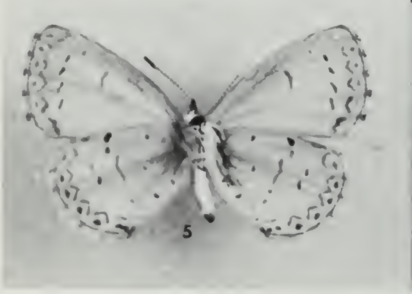
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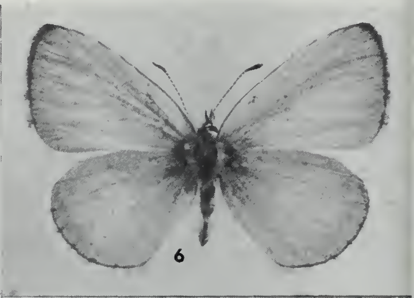
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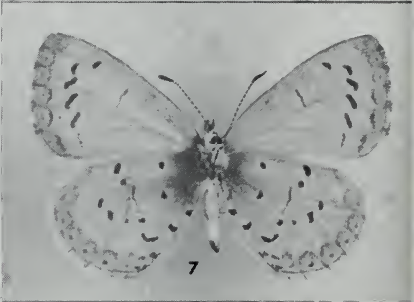
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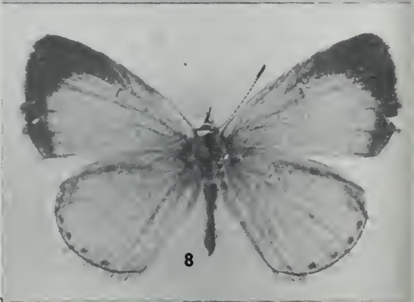
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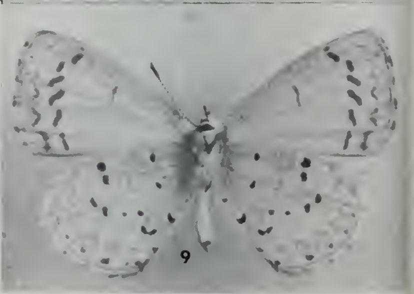
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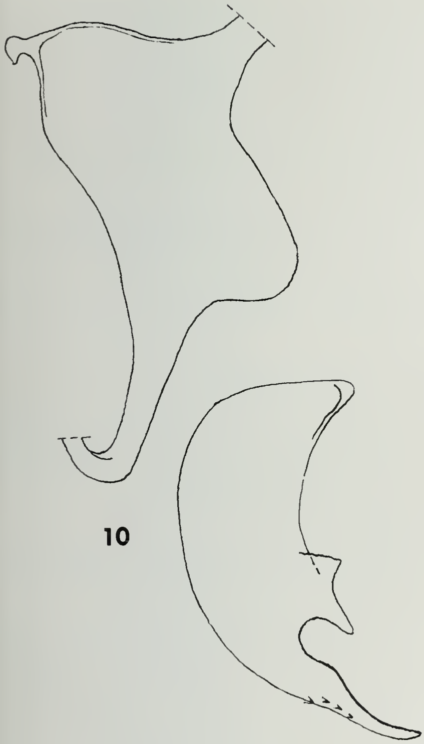

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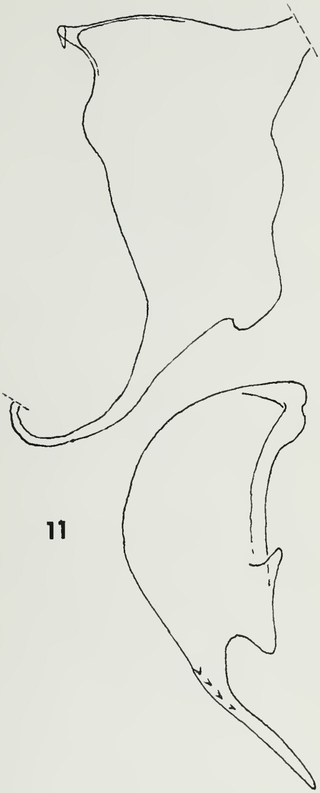

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Fig. 10. *Celastrina ebenina,* n. sp., ♂ genitalia. Preparation C-756, Pittsburgh, Allegheny Co., Pa., 2.vi.1908, collector unknown. The top illustration is the right side of the genital ring, from about the dorsal midline (top dashed line) to just beyond the ventral limit (bottom dashed line). The bottom figure is the left valva. Fig. 11. *Celastrina pseudargiolus pseudargiolus,* summer form, ♂ genitalia. Preparation C-784, 8 mi S of Columbus, Chattahoochee Co., Ga., 2.vii.1944, *leg.* H. K. Clench. Structures shown are the same as in fig. 10.

Fig. 2. *Celastrina ebenina,* n. sp., ♂. [5 mi N of] New Brighton, Beaver Co., Pa., 10.iv.1903, *leg.* H. D. Merrick. Fig. 3. Underside of preceding specimen. Fig. 4. *Celastrina ebenina,* n. sp., ♀. [5 mi N of] New Brighton, Beaver Co., Pa., 13.v.1900, *leg.* H. D. Merrick. Fig. 5. Underside of preceding specimen. Fig. 6. *Celastrina pseudargiolus pseudargiolus,* spring form "violacea," ♂. Oak Station [= vic. Mt. Lebanon], Allegheny Co., Pa., 20.iv.1902, *leg.* F. Marloff. Fig. 7. Underside of preceding specimen. Fig. 8. *Celastrina pseudargiolus pseudargiolus,* spring form "violacea," ♀. Oak Station, Allegheny Co., Pa., 2.v.1906, *leg.* F. Marloff. Fig. 9. Underside of preceding specimen.

REMARKS

Celastrina ebenina appears to be single brooded and flies in the early spring, at about the same time as *C. p. pseudargiolus,* spring brood "violacea."

COMPARISON WITH "violacea": Since "violacea" flies at the same time and in the same places as *ebenina,* and since "violacea" resembles *ebenina* more than any other form of *pseudargiolus* does, I give here a detailed comparison of the two (compare figs. 2 to 5, *ebenina,* and 6 to 9, "violacea"):

(1) Androconia: present on the forewing upperside in male "violacea" (and all other *pseudargiolus* males), absent in male *ebenina.*

(2) Male upperside ground: blue-violet in "violacea," brown-black in *ebenina.*

(3) Female upperside ground: lustrous, bright violet-blue in "violacea," duller, pale gray-blue in *ebenina.*

(4) Female upperside, forewing costal border: gray to bluish on basal half or two-thirds of costa, and discal cell entirely bright blue, in "violacea"; fuscous all the way to base, and covering most of discal cell, in *ebenina.*

(5) Female upperside, forewing terminal fuscous border: thin (covers outer fourth of vein M_3) in "violacea," thick (covers outer third of M_3) in *ebenina.*

(6) Female upperside, basal areas of both wings: blue in "violacea," fuscous in *ebenina.*

(7) Female upperside, cell-end bar of forewing: absent, faint or short (costal half of cell-end), rarely long, in "violacea"; always strong and long in *ebenina.*

(8) Female upperside, cell-end bar of hindwing: absent in "violacea" (and virtually so in all other *pseudargiolus* forms), strong and long in *ebenina.*

(9) Female upperside, costal border of hindwing: bluish gray, darkening to fuscous narrowly along costa in "violacea," heavy fuscous from costa inward to costal cell-vein and usually to M_1 in *ebenina.*

(10) Female upperside, terminal border of hindwing: only a row of small adterminal fuscous spots in "violacea," a row of large adterminal fuscous spots and a thick subterminal fuscous band in *ebenina.*

(11) Female upperside, veins in blue areas of both wings: concolorous with blue ground in "violacea," narrowly fuscous in *ebenina.*

(12) Both sexes underside, adterminal spots of hindwing: minute points, usually fading costad, in "violacea," about twice as large, and not fading costad, in *ebenina.*

(13) Both sexes underside, "marginata"-like blurring (infuscation) of marginal pattern elements, especially of hindwing: absent to slight, rarely moderately strong, in "violacea," absent completely in *ebenina.*

REGIONAL VARIATION: There is some indication that minor differences in the upperside pattern of the females may exist among different populations of *ebenina.* In West Virginia (Coalburg, 7♀ seen), the blue ground is usually uniform (lightened discally on the forewings of one specimen) and the blue lunules in the hindwing terminal border are thick; in western Pennsylvania (3♀ seen) the blue ground is uniform but the blue lunules are usually thin; in Ohio (Vinton Co., 2♀ seen) the blue ground is lightened almost to white in the disc of the forewings and distally on the hindwings, and the blue lunules of the hindwing are thick. Larger series are needed to determine whether or not these differences are constant.

KNOWN LOCALITIES

PENNSYLVANIA: Allegheny Co.: Allegheny [Pittsburgh North Side], *leg.* Herman Lippold, *ex coll.* Henry Engel (1♂, CM); Pittsburgh, 25.iv-10.v, all 1900-1901, *leg.* Frank Knechtel, George Ehrmann, and Henry Engel (4♂2♀, CM).—Beaver Co.: no further data, 14, 21.iv [no year], *leg.* Henry Engel (3♂, CM); New Brighton [5 mi N, see Engel 1908*], 10.iv-13.v, 1900-1905, all *leg.* H. D. Merrick, *ex coll.* H. Engel (1♂, CM) and *ex coll.* Acad. Nat. Sci., Philadelphia (6♂1♀, CM).—Lawrence Co.: Slippery Rock Creek, 5.v.1961, *leg.* J. Bauer and H. Clench (1♂, CM); same, 11.v.1961, *leg.* J. Bauer (1♂, CM).

OHIO: Vinton Co.: 2.5 mi E Zaleski, 10.v.1970, *leg.* H. Clench (3♂ 2♀, CM).

INDIANA: Wabash Co.: "The black male, var. *nigra* of *violacea*, has been taken by the writer in Wabash County, but is not reported elsewhere." (Blatchley 1892*)

MARYLAND: Washington Co.: nr. Sandy Hook [across the Potomac R. from Harper's Ferry], 9.iv.1968, 16.iv.1970, *leg.* John Mason (2♂, CM).

VIRGINIA: Frederick Co.: "western Frederick Co. (not common)" and "west of Cross Jct. on the West Virginia line," 24.iv.1938 (Clark & Clark 1951*).

WEST VIRGINIA: Pendleton Co.: vic. Franklin, 3-5.v.1952 and 28.iv.1954, *leg.* S. S. Nicolay (2♂2♀, CM).—Kanawha Co.: Coalburg (see type series of *ebenina*).

NORTH CAROLINA: Buncombe Co.: road no. 2178, 3100 ft., ca. 6 mi SSE Barnardsville, 29.iv.1972, *leg.* R. E. Price, Jr. (2♂, CM). Edwards (1883*: 87) stated that according to H. K. Morrison the "black form" [*ebenina*] occurred in North Carolina, but until Mr. Price's material came to hand I knew of no documenting specimens.

DOUBTFUL LOCALITIES

NEW YORK: vic. New York City (Scudder 1889*).

TENNESSEE: Vaguely attributed to this state, North Carolina, and Georgia by Edwards (1883*: 87) and repeated in Edwards (June 1884*) and Scudder (1889*). I know of no specimens, but in the light of Price's discovery of *ebenina* in North Carolina, its presence in Tennessee becomes much more probable.

GEORGIA: See preceding.

COLORADO: Edwards (1883*; June 1884*) records a "melanic male" taken by Morrison in southern Colorado. A male of *ebenina* so labeled is in the Edwards collection and documents this, but I strongly suspect that this specimen was somehow accidentally mislabeled. Morrison's shipment reached Edwards in the middle of the latter's great interest in and study of *pseudargiolus* and its forms (cf. Edwards 1883*, prefatory note) and one of Edwards's specimens might well have gotten accidentally into the Morrison lot. Brown, Eff & Rotger [1954-1956 (1955): 176] do not mention *ebenina*, nor have I ever seen another Colorado specimen.

DISTRIBUTION AND HABITAT

As the above records indicate, *ebenina* occurs in a small area (fig. 12) from central Maryland west to Indiana and from just north of Pittsburgh south to the mountains of North Carolina. Within this area *ebenina* is intensely local and colonies are few, although undoubtedly more numerous than we know. Within this same area (and beyond) *C. pseudargiolus* is almost ubiquitous in and near wooded areas. Where something is known of their environments, the localities where *ebenina* occurs are all cool, moist, forested ravines. *Trillium grandiflorum* seems to be a common, perhaps universal, constituent of the habitats and is in flower when *ebenina* is flying. This description holds specifically for the Washington Co., Maryland, record; the Pendleton Co., West Virginia, record; the Lawrence Co., Pennsylvania, record; the Buncombe Co., North Carolina, record; and the Vinton Co., Ohio, record. Such ravines are fairly common in the Pittsburgh area and near Coalburg, West Virginia, so it is reasonable to suppose that *ebenina* was taken in similar environments in those areas. Nothing is known of its habitat in other localities.

A striking parallel to *ebenina* in many of its attributes is the Ravine

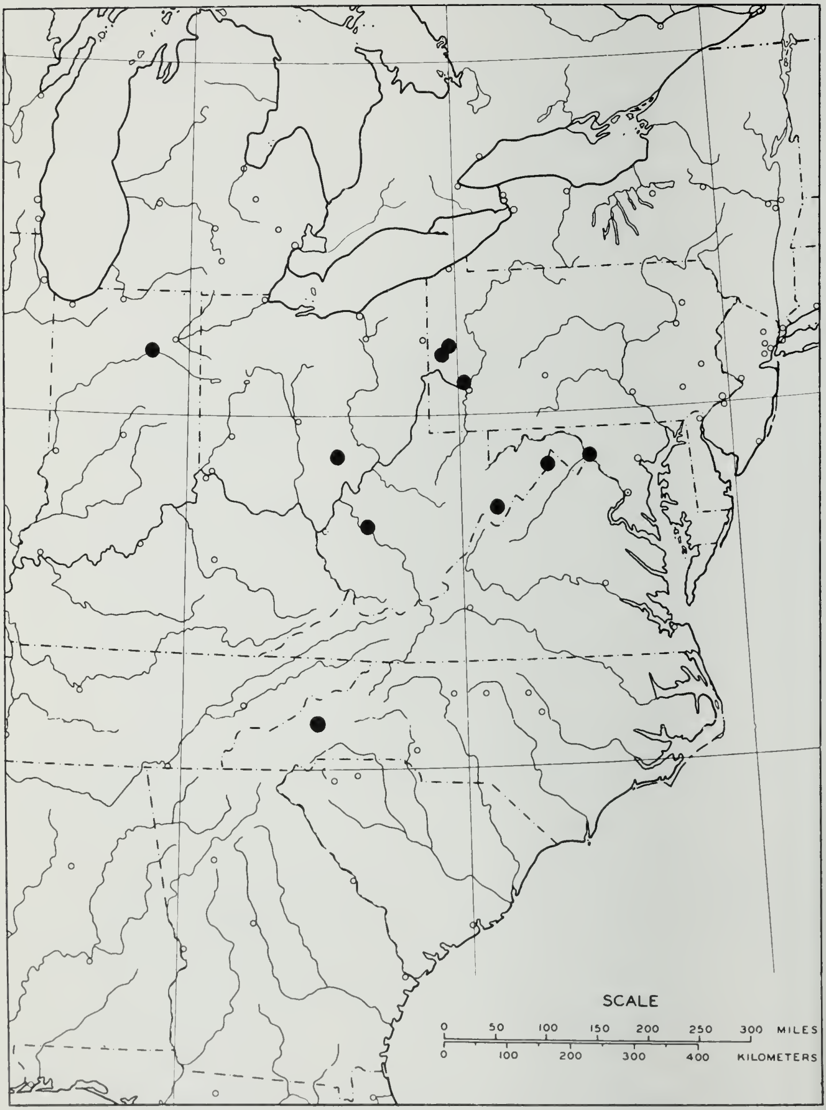

Fig. 12. Known distribution of *Celastrina ebenina*, n. sp.

Salamander, *Plethodon richmondi* Netting & Mittleman (1938), named after my colleague Neil D. Richmond, Curator of Environmental Studies at Carnegie Museum. Mr. Richmond informs me that their distributions are remarkably similar [compare *P. richmondi* (Highton 1962; Highton & Worthington 1967) and *ebenina* (fig. 12)]. Like *ebenina, P. richmondi* occurs in cool, forested ravines (Netting & Mittleman 1938; Highton & Worthington 1967) and is quite local in occurrence. *P. richmondi,* further, is extremely similar to and geographically sympatric with a common, widespread, polymorphic species, *Plethodon cinereus* (Green), with which it was long supposed to be conspecific. At this point I can neither explain this many-sided analogy nor put it to any speculative use, but it is too interesting to omit.

STATUS

Whether *ebenina* is a form of *pseudargiolus,* as heretofore believed, or a full species is a question central to the present paper and important biologically. It needs careful consideration.

More than tradition supports the hypothesis that *ebenina* is simply a morph of *pseudargiolus.* It resembles the regional spring form "violacea" of nominate *pseudargiolus* closely on the underside, and wherever *ebenina* has been taken "violacea" has been found with it in the strictest sense. The small colony of *ebenina* that I found in Ohio occupied only a small area, perhaps no more than a hundred by twenty or thirty feet, yet in precisely the same area I also took two female "violacea," and I saw neither "violacea" nor *ebenina* anywhere else in that vicinity. The male genitalia appear to be inseparable from those of sympatric *pseudargiolus,* all the more significant since the male genitalia of *pseudargiolus* show minor but constant geographical variation.

The hypothesis that *ebenina* is a full and independent species is, however, supported by numerous points and in my opinion these far outweigh the preceding factors. First, the pattern of *ebenina* is consistently and strikingly different, not just on the upper surface but also in minor details of the under surface (notably the enlarged adterminal spots of the hindwing) in both sexes. Second, males completely lack the androconial scales on the upper surface that are always found in male *pseudargiolus.* Third, *ebenina* is differentiated from "violacea" by multiple traits and no intermediates between the two are known. Fourth, the distribution of *ebenina* suggests a species far more than a form: its range is small, while that of *pseudargiolus* is vast; within its area *ebenina* is extremely local, while within the same area *pseudargiolus* is virtually ubiquitous in wooded places; and yet, despite the intense localization of *ebenina,* when one finds a colony the individuals are usually rather numerous. Fifth, there is some evidence that locally *ebenina* has a flight period slightly later than that of *pseudargiolus.*

This is suggested by Edwards's (1869*) remarks (". . . for the females do not appear until some days after [the males] . . . Most of the females are of the black type [*i.e., ebenina* ♂] . . ."), and by the condition of the specimens of both *ebenina* and *pseudargiolus* that I took together in Ohio. Finally, the possible minor geographic variation of *ebenina* briefly described above is consistent with the hypothesis of a distinct species dispersed in small, widely separated colonies between which gene flow must be extremely low at best. The populations of *pseudargiolus* are much more panmictic and show no local geographic differentiation on this small scale.

ACKNOWLEDGMENTS

I am grateful to the following for their assistance: Mr. F. Martin Brown, for reading and commenting on an early draft of the manuscript and for taking the photographs that illustrate this paper; Dr. John Mason, Kensington, Maryland, Mr. S. S. Nicolay, Virginia Beach, Virginia, and Mr. R. E. Price, Jr., Mars Hill, North Carolina, for furnishing additional locality records of *ebenina* and for their generous gift of exemplary specimens to Carnegie Museum; Mr. Neil D. Richmond, Curator of Environmental Studies, and Dr. Clarence J. McCoy, Jr., Curator of Amphibians and Reptiles, Carnegie Museum, for valuable discussion and help with the herpetological literature.

REFERENCES CITED

Text references in which the year is followed by an asterisk (*) are given in the synonymy of *C. ebenina.*

BROWN, F. MARTIN, D. EFF AND B. ROTGER
1954-1956. Colorado butterflies. Denver Mus. Nat. Hist., Proc., 3-7: viii + 368 pp., ill.

HIGHTON, RICHARD
1962. Revision of the North American salamanders of the genus Plethodon. Bull. Florida State Mus., 6: 235-367, ill.

HIGHTON, RICHARD, AND RICHARD D. WORTHINGTON
1967. A new salamander of the genus *Plethodon* from Virginia. Copeia, 1967: 617-626, ill.

HOLLAND, W. J.
1915. The butterfly guide. Garden City, N.Y., Doubleday, Page, 237 pp., ill.

INTERNATIONAL TRUST FOR ZOOLOGICAL NOMENCLATURE
1964. International Code of Zoological Nomenclature (ICZN). London, xx + 176 pp.

NETTING, M. GRAHAM, AND M. B. MITTLEMAN
1938. Description of Plethodon richmondi, a new salamander from West Virginia and Ohio. Ann. Carnegie Mus., 27 (18): 287-293.

SHAPIRO, ARTHUR M.
1966. Butterflies of the Delaware Valley. Special Publ., American Ent. Soc. (Philadelphia): vi + 79 pp., ill.

STRECKER, HERMAN
1872-1900. Lepidoptera, rhopaloceres and heteroceres, indigenous and exotic; with descriptions and colored illustrations. Reading, Pa. (author): 143 pp., ill., plus Suppl. 1 (12 pp.), 2 (11 pp.), and 3 (37 pp.).

ANNALS
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THE LATE PLEISTOCENE SMALL MAMMALS OF EAGLE CAVE, PENDLETON COUNTY, WEST VIRGINIA

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Field Associate

Section of Vertebrate Fossils

NATURAL HISTORY SURVEY
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Location

Eagle (Eagle Rock) Cave, Pendleton County, north-central West irginia (long 79° 17′ W, lat 38° 50′ N, elevation 2500 feet, Onego Quad. .S.G.S. 15′ series), is the smallest of several caves in the New cotland-Coeymans Member of the Helderburg Limestone at the outhern end of Cave Mountain (fig. 1). Eagle Cave, about 100 eet below the crest of the mountain, some 1000 feet above the oor of Smokehole Valley, overlooks the South Branch of the otomac River. High Knob, North Fork Mountain, about three miles est of the cave, rises to a height of almost 3800 feet, some 2300 feet igher than the river. Cave Mountain lies in the Ridge and Valley Province, just east of the Allegheny Front, in one of the most rugged secions of the West Virginia mountains, surrounded by the Monongahela ational Forest. The major Cave Mountain caves are discussed in avies, 1965; Eagle Cave is not.

The cave faces west across the river valley, opposite Dry Hollow nd the north end of Pretty Ridge. The valley of the South Branch t this point, and for many miles downstream, i.e., to the north, is hysiographically young, narrow, and tortuous. Directly south of the

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ubmitted for publication May 1, 1972.

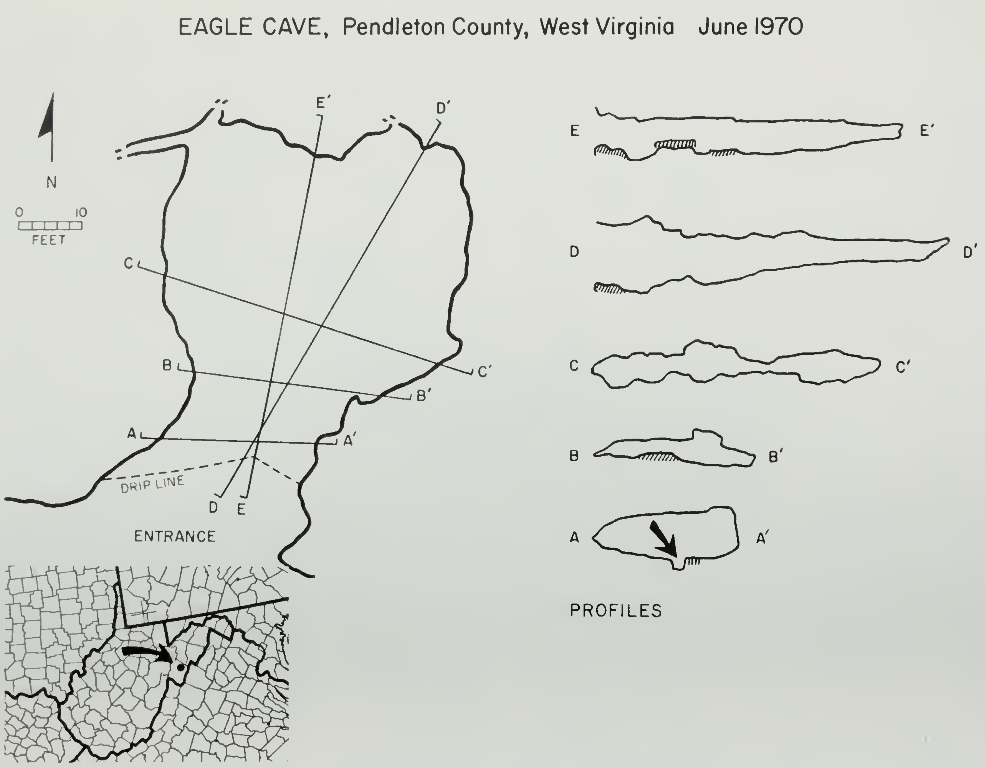

Fig. 1. Map of Eagle Cave, Pendleton County, West Virginia. Arrow in profile A—A′ points to Carnegie Museum excavation. Arrow on insert map, lower left, points to Pendleton County and location of cave.

cave, upstream, the river enters this valley from the east, through the Big Mountain/Cave Mountain gap, from a broad, flat, physiographically older valley. Apparently the South Branch of the Potomac was pirated sometime in the past, its headwaters captured by Smokehole Valley drainage.

DESCRIPTION

Eagle Cave has seen much traffic through the years. There is a picnic area at the base of the mountain at Eagle Rock, and people walk the trail from time to time to visit Cave Mountain in the same outcrop. As a consequence, the floor of Eagle Cave has been badly disturbed. The cave has an entrance about 20 feet wide and seven feet high, and is about 50 feet deep and 40 feet wide. Its height diminishes sharply from front to rear. The floor is littered with breakdown from the roof (fig. 2) and slopes gently in from the cave mouth, where once there had apparently been a talus build-up which has been eroded away. The cave floor at this point had been protected from disturbance for some time by a large ceiling spall weathered on its upper side (fig. 3). This 500-pound rock was removed and a hole four-feet square and from two to three feet deep was excavated o bedrock in the center of the cave immediately behind the drip line. Only a small portion of the total cave floor was excavated (fig. 1). Approximately three-fourths of a ton of matrix was removed by one-foot levels. No evidence of stratification or faunal change with depth was noted—all materials were combined. Matrix was colored deep red to brown, was highly compressed, and appeared to have ittle moisture in it. It derived from breakdown products of the limestone as well as from erosion debris from higher on the mountain. Approximately 5% of the matrix was composed of small rock fragments from one-fourth inch to one inch in diameter, with occasional arger ones up to five inches in length. All appeared to be of native rock, frost-wedged from the ceiling or walls. Small mammal bones and teeth occurred, sparsely throughout, badly fragmented and with no apparent orientation.

The face of the mountain below the cave is strewn with breakown from the cave outcrop. The cave mouth in the outcrop faces he prevailing westerlies and is exposed to the full rigor of the weather. Erosion is active, and in a relatively short time any original matrix in this shallow cave will have been eroded away. The floor f the cave is starting to break up near the entrance now.

High on a rocky promontory, this deposit of vertebrate remains has accumulated primarily by raptorial birds. The position of the ave makes it an ideal aerie. Only through the action of wide-ranging octurnal birds of prey could such a diverse small mammal fauna,

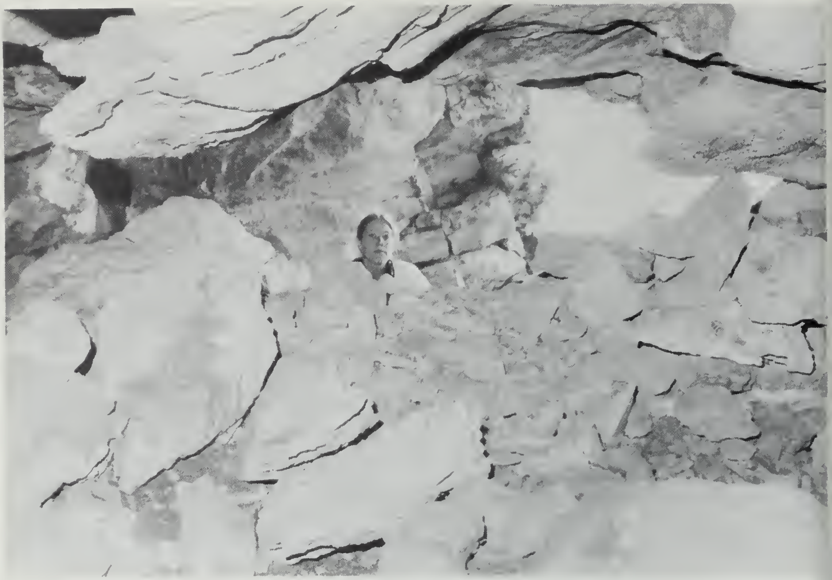

Fig. 2. View toward entrance from rear of Eagle Cave, Pendleton County, West Virginia. Note extensive roof breakdown.

obviously removed from both field and forest situations, accumulate in this out-of-the-way situation. Such birds habitually regurgitate undigested bone in and around their nests, and this in time becomes incorporated into accumulating cave-floor deposits.

A Carnegie Museum field party, led by Hamilton, excavated the site from June 25 to July 6, 1970. We wish to thank Helen and Paul Imblum, Janet and Allen Bailey, Lee Ambrose, Timmy Clair, Rita Hamilton, Allen Hamilton, and Ann Rhunka for their help in excavating this difficult mountain cave, and Charles Schwab for transporting the excavated matrix to the Museum field laboratory at New Paris, Pennsylvania. Research was conducted under National Science Foundation Grant no. GB18706X, made to the senior author.

The abbreviation CM in Table 1 refers to Carnegie Museum. Omission of the degree symbol in temperature readings (e.g., "6—7 F") follows the *Style Manual for Biological Journals* standard.

ENVIRONMENT

The topography of the area is controlled by its geology. The long parallel mountain ridges are of erosion-resistant sandstones, the intermontane valleys less resistant shales and limestones. The Potomac River cuts across the mountain ranges from west to east and apparently

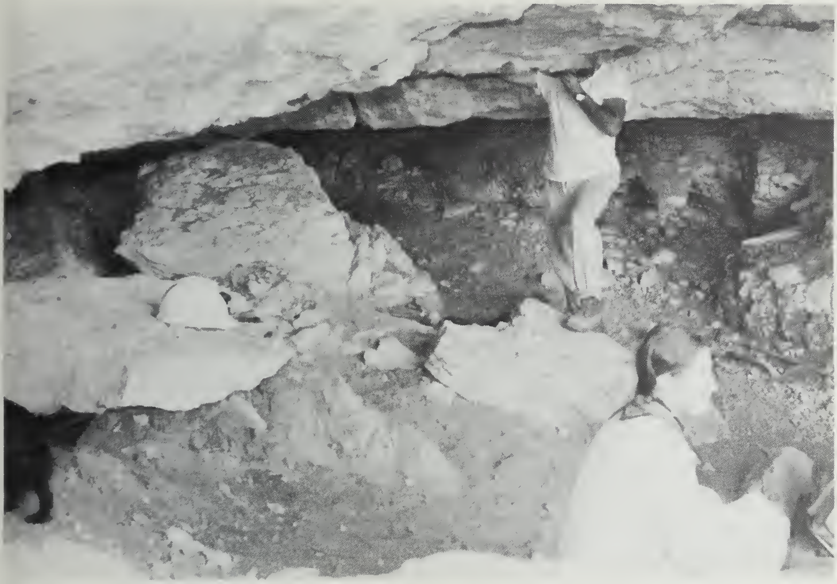

Fig. 3. View into Eagle Cave, Pendleton County, West Virginia, taken from point D (see fig. 1). Note extensive roof breakdown. Man in background stands behind roof spall that was removed prior to excavation.

predates their formation, but its tributaries form parallel branches to the northeast and the southwest following the present valley floors.

Local climate is variable. Annual rainfall on the Allegheny Plateau, 10 miles west of Eagle Cave, varies from 40 to 50 inches per year. Immediately to the east, the Ridge and Valley Section in the rain shadow of the Plateau averages some 10 inches less per year. In 1930, the driest season on record, precipitation was less than 20 inches at some locations on the Plateau. The temperature of the Ridge and Valley Section averages 6 to 7 F higher than that of the summits of the Allegheny Plateau. Clarkson (1966) states that the lowest recorded temperatures are —37 F at Lewisburg, Greenbrier County, and —30 F at Bayard, Grant County. The highest recorded temperature from the Ridge and Valley Section was 104 F. The average growing season on the Plateau is 119 to 145 days, and in the adjacent Ridge and Valley Section, 147 to 150 days. Killing frosts have been reported as late as June 17 and as early as September 10 in some mountain localities.

Prevailing winds are from the west. Much of their moisture is lost as precipitation as they pass over the high Allegheny Plateau, and they become warmer and drier as they reach the Ridge and Valley Section. This difference is significant in the distribution of the flora today.

TABLE 1

EAGLE ROCK LOCAL FAUNA, PENDLETON COUNTY, WEST VIRGINIA

Species	Minimum Number Animals		Level		Minimum Based on:	CM Catalog Number
		1	2	3		
Class OSTEICHTHYES						
small fish	sparse	X	X	X	vertebra	24424
Class AMPHIBIA and REPTILLIA						
small snake, toad/frog	sparse	X	X	X		24429
Class MAMMALIA Linnaeus, 1758						
Order INSECTIVORA Bowdich, 1821						
Family: Soricidae Gray, 1821						
Sorex arcticus Kerr *arctic shrew	1	—	—	X	mandible	24401
Sorex cf. *fumeus* Miller smoky shrew	1	X	—	—	tibia	24400
Blarina brevicauda (Say) short-tailed shrew	7	X	X	X	mandible	24397-24399
Cryptotis parva (Say) least shrew	1	—	—	X	mandible	24421
Family: Talpidae Gray, 1825						
Parascalops breweri (Bachman) hairy-tailed mole	1	X	X	—	mandible	24413-24414
Order CHIROPTERA Blumenbach, 1779						
Family: Vespertilionidae Gray, 1821						
Myotis, ?species a (smaller than b)	1	—	X	—	mandible with M_3	24419
Myotis, ?species b (larger than a)	2	—	—	X	mandible. P_4—M_1; M_2	24420
Myotis Kaup, unassignable fragments	1	X	—	—	M_1	24418

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*Not extant in West Virginia since beginning of Colonial times.

TABLE I

EAGLE ROCK LOCAL FAUNA, PENDLETON COUNTY, WEST VIRGINIA (continued)

Species	Minimum Number Animals	Level 1	Level 2	Level 3	Minimum Based on:	CM Catalog Number
		Order LAGOMORPHA Brandt, 1855				
		Family: Leporidae Gray, 1821				
Leporidae, ?species	1 +	X	X	X	isolated teeth	24423
		Order RODENTIA Bowdich, 1821				
		Family: Sciuridae Gray, 1821				
Marmota monax (Linnaeus) woodchuck	*2*	—	X	—	isolated teeth	24396
Spermophilus tridecemlineatus (Mitchill) *thirteen-lined ground squirrel	*1 or 2*	X	X	—	isolated teeth	24391-24393
Tamiasciurus hudsonicus (Erxleben) red squirrel	*2*	X	X	—	P_4	24389-24390
Glaucomys cf. *sabrinus* (Shaw) northern flying squirrel	*1*	—	X	X	maxilla	24394-24395
		Family: Cricetidae Rochebrune, 1883				
Peromyscus Gloger, ?species probably *P. leucopus* or *P. maniculatus*	*3*	—	X	X	mandible	24416-24417
Neotoma floridana (Ord) woodrat	*7*	X	X	X	M_1	24402-24403, 24415
Clethrionomys gapperi (Vigors) red-backed vole	*4*	X	X	X	M_1	24371, 24379, 24386
Phenacomys cf. *intermedius* Merriam *spruce vole	*1*	—	—	X	M^2	24381
Microtus pennsylvanicus (Ord) meadow vole	*1*	—	X	—	M^3	24376
Microtus chrotorrhinus (Miller) rock vole	*2*	—	X	X	M^3	24373, 24384
Microtus pennsylvanicus or *M. chrotorrhinus*	*8*	X	X	—	M_1	24372, 24374, 24383

*Not extant in West Virginia since beginning of Colonial times.

TABLE 1

EAGLE ROCK LOCAL FAUNA, PENDLETON COUNTY, WEST VIRGINIA (continued)

Species	Minimum Number Animals	Level			Minimum Based on:	CM Catalog Number
		1	2	3		
Microtus xanthognathus (Leach) *yellow-cheeked vole	1	—	X	—	mandible	24377, 24388
Microtus (Pitymys) pinetorum (Le Conte) pine vole	7	—	X	X	M_1	24375, 24385
Synaptomys cooperi Baird southern bog lemming	1	X	—	—	M_1	24370
Synaptomys borealis (Richardson) *northern bog lemming	1	—	—	X	M_1	24382
Ondatra zibethicus (Linnaeus) muskrat	1	—	X	X	M_2	24380, 24387
Family: Zapodidae Coues, 1875						
Zapus hudsonius (Zimmerman)? meadow jumping mouse ?	1	X	—	—	upper incisor	24422
Family: Erethizontidae Thomas, 1897						
Erethizon dorsatum (Linnaeus) +porcupine	1	—	X	—	partial molar	24426
Family: Castoridae Gray, 1821						
Castor canadensis Kuhl beaver	1	—	X	—	dp4	24427
Order CARNIVORA Bowdich, 1821						
Family: Procyonidae Bonaparte, 1850						
cf. *Procyon lotor* (Linnaeus) raccoon	1	—	—	X	canine	24428
Family: Mustelidae Swainson, 1835						
Martes americana (Turton) *pine marten	1	X	—	—	P^4	24425

*Not extant in West Virginia since beginning of Colonial times.

+Not extant in West Virginia now, but may have been living there in Colonial times.

Originally, the thin, acidic, sandy, well-drained soils of Cave Mountain supported a chestnut/oak forest. The original vegetation of the Ridge and Valley Section, however, is poorly known. The forests along the major streams were destroyed before their composition could be studied. Clarkson (1966:8) states, "On the drier slopes of this section the dominant trees were chestnut [*Castanea*] and chestnut oak [*Quercus prinus*] with mixtures of other oaks . . . In the more mesic situations were found a variety of hardwoods, mainly yellow poplar [*Liriodendron*], hemlock [*Tsuga*], red oak [*Quercus rubra*], white oak [*Quercus alba*], and basswood [*Tilia*] with white oak being the most characteristic tree." At altitudes of 2000 to 2500 feet, northern hardwoods formed a narrow belt on the mountain slopes above the oak/chestnut and below the spruce *(Picea),* composed mainly of yellow birch *(Betula lutea),* sugar maple *(Acer saccharum),* red maple *(A. rubrum),* beech *(Fagus),* and basswood. Along the higher mountains, e.g. North Fork Mountain, 3 miles west of the cave, stands of red spruce *(Picea rubens)* are, or were, found at elevations above 2500 feet. Clarkson (1966:10) writes. "Spruce flourished where the soil and atmospheric moisture were abundant and was able to compete at higher elevations on thin, moist soil with the more exacting species." Grass/sedge meadows occasionally occurred in poorly drained mountain valleys and may well have persisted from late Pleistocene times.

FAUNA

The remains of small fish, frogs, snakes, five species of insectivores, three of bats, 18 of rodents, one lagomorph, and two carnivores were recovered from the excavation. In all, these remains represented a minimum of 68 individual mammals. Porcupine and immature beaver, the largest mammals in the collection, were represented by isolated molars; the smaller rodents and insectivores by upper or lower dentitions or isolated teeth. Remains of larger mammals were conspicuously absent. The cave at no time appears to have formed a natural trap, and the faunal remains are confined to animals small enough to form owl prey. Some of the species, bats and woodrat, probably inhabited the cave, but the presence of nocturnal field and forest forms, and the high number of microtines suggests the activity of owls.

The Eagle Cave local fauna is but one of a number of geographically widespread fossil faunas of Rancholabrean age from the central Appalachians and flanking plateau and piedmont regions. These local faunas have in common a number of Recent Canadian and Hudsonian Life Zone small mammals that occupied the area during some phase of the Wisconsinan glaciation.

The yellow-cheeked vole *(Microtus xanthognathus)* (fig. 4 top), the northern bog lemming *(Synaptomys borealis),* the heather vole *(Phenacomys intermedius),* and the arctic shrew *(Sorex arcticus)*

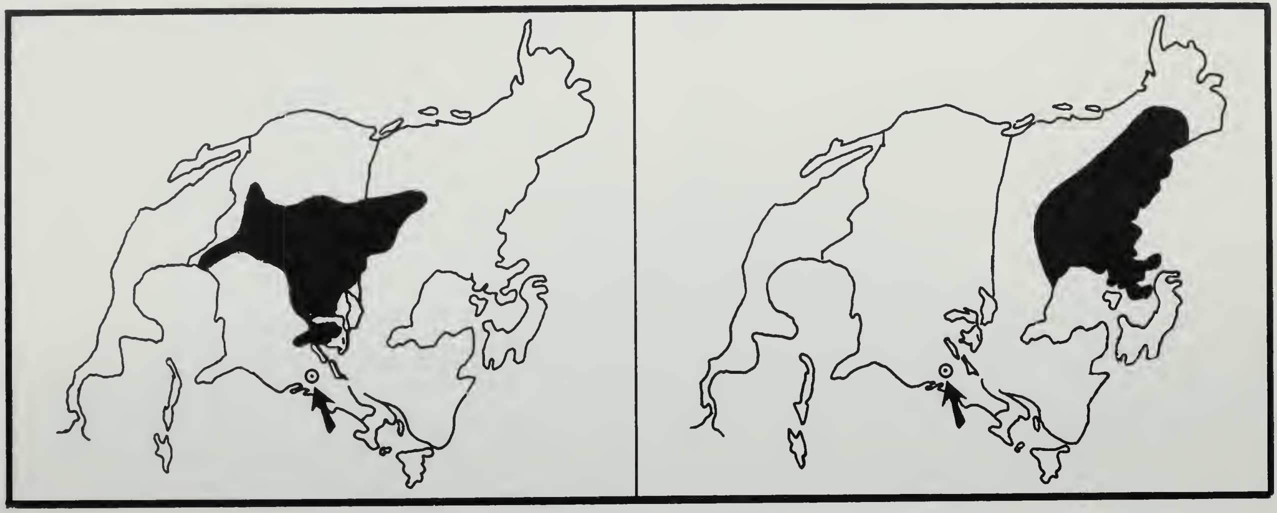

Fig. 4. Upper map: North American range of yellow-cheeked vole [*Microtus xanthognathus* (Leach)]. Arrow points to Eagle Cave, Pendleton County, West Virginia. Lower map: North American range of thirteen-lined ground squirrel [*Spermophilus tridecemlineatus* (Mitchill)]. Arrow points to Eagle Cave.

are species that have since retreated to the north. *Synaptomys borealis,* occurring as far south as northern New England, is the only one of these species still found in the Appalachian Mountains. Remains of these small mammals had not hitherto been recovered from West Virginia, but they form a characteristic element of the early post-Wisconsinan cave deposits of the central Appalachians [New Paris No. 4, Pa., 96 miles to the north (Guilday *et al.,* 1964); Bootlegger Sink, Pa., 162 miles northeast (Guilday *et al.,* 1966); Natural Chimneys, Va., 36 miles southeast (Guilday, 1962); Welsh Cave, Ky., 315 miles west of Eagle Cave (Guilday *et al.,* 1971)]. Two of these local faunas (New Paris No. 4, Pa., Welsh Cave, Ky.) have carbon-14 dates of 11,300 ± 1000 yrs. B.P. (Y-727) and 12,950 ± 550 yrs. B.P. (I-2982).

Another species characteristic of such sites is the thirteen-lined ground squirrel *(Spermophilus tridecemlineatus).* At present it is confined to prairie areas of central North America as far north as southern Canada, and as far east as western Ohio (fig. 4 bottom). The valley of the South Fork of the Potomac, below Eagle Cave, narrow, precipitous, physiographically young, does not appear to have been suitable for grasslands. A few miles upstream, however, as noted above, the river flows through a wide, physiographically older valley whose floor may well have supported grassland features.

Although most other species identified from the Eagle Rock local fauna inhabit the state today, the porcupine and pine marten may have been exterminated during Colonial times. The rock vole *(Microtus chrotorrhinus)* is at present a boreal relict form occurring sporadically in high mountain rocky situations along the crest of the Appalachians as far south as Georgia. It has been recorded as close as 16 miles southwest of the cave, on Spruce Knob, elevation 4700 feet, but has been taken as low as 2750 feet in Greenbrier County (McKeever, MS). The northern flying squirrel *(Glaucomys sabrinus),* the porcupine *(Erethizon dorsatum),* and the pine marten *(Martes americana)* were of limited distribution, confined for the most part to high Canadian Zone forests. The red-backed mouse *(Clethrionomys gapperi)* is another forest animal, ostensibly boreal but less exacting in its requirements. It would be available as prey in the area today. All other species are of wide distribution within the area today.

The presence of the least shrew *(Cryptotis parva),* represented by one lower jaw from the 3-foot level of the excavation, was unexpected. The presence of this primarily southern field form is not in keeping with the boreal aspect of the fauna and may indicate that the deposit accumulated over a long period, incorporating both boreal and temperate elements. But the range of the least shrew and that of the thirteen-lined ground squirrel overlap in a broad area of the north-central United States as far north as southern Minnesota (Hall &

Kelson, 1959), so it is conceivable that the two may have shared the same local grasslands habitat during late Pleistocene times. Both were also present in the Natural Chimneys and Bootlegger Sink local faunas.

Climatic effects most certainly varied with latitude. This appears to be demonstrated by a progressive dropout of some of the small mammals characteristic of these Wisconsinan boreal faunas. The collared lemming *(Dicrostonyx hudsonius),* for instance, has been recorded no farther south than latitude 40° N (New Paris No. 4, Pa.); *Microtus xanthognathus* no farther south than latitude 38° N (Natural Chimneys, Va.). *Synaptomys borealis* and *Phenacomys* occur as far south as latitude 36½° N (Baker's Bluff, Tenn.). West of the Appalachians proper, *M. xanthognathus* occurs at latitude 38° N (Welsh Cave, Ky.), but apparently not as far south as latitude 36° N [Robinson Cave, Tenn. (Guilday *et al.,* 1969)].

Most of these cave faunas have no accompanying large mammal remains because of the circumstances of accumulation and preservation (fossil owl roosts and narrow fissure traps). The several large-mammal concentrations, fluvial and bog, rather than cave deposits, dating from Wisconsinan and early post-Wisconsinan times, rarely possess a small-mammal component [Saltville, Va. (Ray *et al.,* 1967), Big Bone Lick, Ky. (Schultz *et al.,* 1963)]. But these sites are contemporaneous within the broad framework of the Wisconsinan glaciation. The discrepancy shown by the altogether Recent aspect of the small mammals and the high number of extinct large mammals highlights the peculiar nature of the faunistic change that took place approximately 10,000 years ago, when the large mammals were swept by a wave of extinctions that apparently had no effect on the small-mammal component of such faunas.

These Wisconsinan local faunas can be distinguished in the Appalachians from an earlier fauna, pre-Wisconsinan in age and probably Illinoian [Cumberland Cave, Md., for instance (Gidley & Gazin, 1938)]. This earlier fauna is characterized by a high rate of extinction, in contrast to Wisconsinan faunas, of both the large and the small mammal component. The earlier fauna appears to be more continental in composition, containing such forms as pika *(Ochotona)* and western pocket gopher [*Thomomys (Plesiothomomys)*], which seem to be absent from later faunas. The microtines are of primitive aspect. *Neofiber* and *Ondatra annectens* are present, *O. zibethicus* is not. *Atopomys* is present. The progressive forms of *Microtus* (those possessing five closed alternating triangles in M_1) that now inhabit the Appalachians *(M. pennsylvanicus, M. chrotorrhinus),* or did in Wisconsinan times *(M. xanthognathus),* are absent from these Illinoian faunas. Instead, forms of *Microtus* with four alternating triangles, a more primitive condition, are found. Many small mammals are common to both, but faunas of these two time horizons are quite distinct in their make-up. Much remains to be done to resolve them and to trace the effects upon these fossil faunas of latitude and climatic change along the thousand miles of the Appalachian Mountain system.

Speculation on the ecological implications of the Eagle Cave local fauna, other than in the broadest sense, would be premature. The physiography of the area is rugged, and even under today's temperate climatic regime the area supports varied and distinct biotic communities, because of the effects of altitude, soil conditions, and local rain shadows. Fluctuations in climatic parameters vary within short distances. The situation during the late Pleistocene was undoubtedly just as diverse under more boreal conditions. The amount of bone recovered from the deposit was insufficient for a carbon-14 date, so that its age can be stated only in general terms. The deposit itself is composed of the remains of both grassland and forest forms. These were not, as in a sinkhole trap situation like New Paris No. 4, Pa., recovered from the immediate vicinity, but from any point within the cruising range of the raptorial birds responsible for the accumulation. The deposit gives only a general impression of some combination of boreal forest and grassland. It tells nothing of the extent of either, however. The picture will no doubt come into clearer focus with additional research. Although low in numbers and variety of vertebrate remains compared with some other Appalachian cave sites like New Paris No. 4, Pa., the Eagle Cave deposit is the first late Pleistocene cave deposit to be reported from the state of West Virginia.

REFERENCES CITED

CLARKSON, R. B.
1966. The vascular flora of the Monongahela National Forest, West Virginia. Castanea, 31:1-119.

DAVIES, W. E.
1965. Caverns of West Virginia. W. Va. Geological and Economic Survey, Morgantown, XIX A: 330 pp. plus 72 pp.

GIDLEY, J. W., AND C. L. GAZIN
1938. The Pleistocene vertebrate fauna from Cumberland Cave, Maryland. U. S. Nat'l. Mus. Bull., 171: 1-99.

GUILDAY, J. E.
1962. The Pleistocene local fauna of the Natural Chimneys, Augusta County, Virginia. Ann. Carnegie Mus., 36: 87-122.

GUILDAY, J. E., H. W. HAMILTON, AND A. D. MCCRADY
1966. The bone breccia of Bootlegger Sink, York County, Pa. Ann. Carnegie Mus., 38: 145-163.
1969. The Pleistocene vertebrate fauna of Robinson Cave, Overton County, Tennessee. Palaeovertebrata (Montpellier), 2: 25-75.
1971. The Welsh Cave peccaries *(Platygonus)* and associated fauna, Kentucky Pleistocene. Ann. Carnegie Mus., 43: 249-320.

GUILDAY, J. E., P. S. MARTIN, AND A. D. MCCRADY
1964. New Paris No. 4: a Pleistocene cave deposit in Bedford County, Pennsylvania. Bull. Nat'l. Speleo. Soc., 26: 121-194.

HALL, E. R., AND K. R. KELSON
1959. The mammals of North America. New York, The Ronald Press Co., 2 vols., 1162 pp.

MCKEEVER, S.
[MS.] Ecology and distribution of the mammals of West Virginia. MS (Ph.D. thesis) on file at North Carolina State Coll., Raleigh, 1954, 335 pp.

RAY, C. E., B. N. COOPER, AND W. S. BENNINGHOFF
1967. Fossil mammals and pollen in a late Pleistocene deposit at Saltville, Virginia. Jour. Paleont., 41: 608-622.

SCHULTZ, C. B., L. G. TANNER, F. C. WHITMORE, JR., L. L. RAY, AND E. C. CRAWFORD
1963. Paleontologic investigations at Big Bone Lick State Park, Kentucky: A preliminary report. Science, 142: 1167-1169.

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BIBLIOGRAPHY, OTTO EMERY JENNINGS

Dorothy L. Pearth
Associate Curator of Plants

Contained here are 302 titles, so far as can be determined a complete list, save for newspaper articles, of the published writings of the late botanist, naturalist, ecologist, and educator Dr. Otto E. Jennings.

Dr. Jennings, born in Olena, Ohio, in 1877, came to Carnegie Museum in 1904 as Custodian of Botanical Collections, and was made Curator in 1915. After a 60-year association with the Museum, he died on January 29, 1964, as Director Emeritus of Carnegie Museum and Professor Emeritus, Department of Biological Sciences, University of Pittsburgh.

For biographies of Dr. Jennings by L. K. Henry, M. Graham Netting, and Adolph E. Waller, see respectively, *Trillia* 12: iii-vi, 1964 (1 photo); *The Bryologist* 68 (3): 353-359, 1965 (1 photo); and *Ohio Journal of Science* 64 (4): 303, 1964.

1901. Notes on abutilons. Jour. Columbus Hort. Soc., 16 (4): 108-110.

1902. Some of the effects of colored light upon plant growth. Jour. Columbus Hort. Soc., 17 (4): 134-138.

Smut infection experiments. Ohio Naturalist, 2 (6): 258-261, 1 fig. (with W. A. Kellerman).

Meeting of the Biological Club [Secretary's Report]. Ohio Naturalist, 3 (1): 322.

1903. Some ecologic factors and their relations to Ohio horticulture. Jour. Columbus Hort. Soc., 18 (2): 50-53.

Some climatic conditions of Ohio. Ohio Naturalist, 3 (3): 339-345, 8 maps, 1 table.

Further notes on some climatic conditions of Ohio. Ohio Naturalist, 3 (6): 403-409, 4 maps.

Meeting of the Biological Club [Secretary's Report]. Ohio Naturalist, 3 (8): 452. (With Robert F. Griggs)

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NATURAL HISTORY SURVEY
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1904. Ecological study of Brush Lake. Proc. Ohio Acad. Sci., 4 (4), Special Paper 10: 147-165, 2 pl. (With J. H. Schaffner and F. J. Tyler)

Report for 1902 on the State herbarium, including additions to the State plant list. Ohio Naturalist, 4 (3): 59-60. (With W. A. Kellerman)

Notes on some rare or interesting Ohio plants. Ohio Naturalist, 4 (3): 61. [Abstract]

Flora of Cedar Point. Ohio Naturalist, 4 (8): 186-190. (With W. A. Kellerman)

Some native shrubs of ornamental promise. Jour. Columbus Hort. Soc., 19 (1): 10-15.

1905. Notes on the vegetable tissues in Daemonclix. Memoirs, Carnegie Mus., 2 (3): 190-191.

1906. Some new or noteworthy species reported for Ohio in recent botanical literature. Ohio Naturalist, 6 (5): 492-495.

Additions to the flora of Cedar Point, II. Ohio Naturalist, 6 (8): 544-545.

A note on the discharge of spores in *Bulgaria rufa*. Mycol. Bull., 4: 257-258.

Additions and corrections to the list of vascular flora of Allegheny County, Pennsylvania. Ann. Carnegie Mus., 3 (4): 473-479.

A new species of Kneiffia (*K. sumstinei*). Ann. Carnegie Mus., 3 (4): 480-481, 1 pl.

A note on the occurrence of *Triglochin palustris* Linnaeus in Pennsylvania. Ann. Carnegie Mus., 3 (4): 482.

A new species of Ibidium (Gyrostachys) (*I. incurvum*). Ann. Carnegie Mus., 3 (4) 483-486, 1 pl.

A new species of Lonicera (*L. altissima*) from Pennsylvania. Ann. Carnegie Mus., 4 (1): 73-77, 1 pl.

1907. A case of poisoning by *Amanita phalloides*. Jour. Mycol., 13: 187-188. A note or the poisonous properties of the yellow ladies' slipper. Plant World, 10: 189-191.

1908. A note on the ecological formations of Pittsburg and vicinity. Science, new ser. 27 (699): 828-830.

A descriptive key to the woody climbing plants commonly cultivated in Ohio Proc. Columbus Hort. Soc., 22: 20-46.

An ecological classification of the vegetation of Cedar Point. Ohio Naturalist, (6): 291-340; figs. 1-22.

A further occurrence of *Wynnea americana* in Pennsylvania. Ann. Carnegie Mus 4 (3-4): 226-227; 1 pl.

1909. *Hymenophyllum denticulatum* in central China. Fern Bull., 17: 106-107, 1 fig.

A botanical survey of Presque Isle, Erie County, Pennsylvania. Ann. Carnegi Mus., 5 (2-3): 289-421, pl. 22-51, figs. 1-4.

Some new or otherwise noteworthy plants from Ohio. Ohio Naturalist, 9 (4): 440 442.

The Labrador tea in Ohio. Ohio Naturalist, 10 (1): 13.

1910. A supplementary description of *Cerastium arvense Webbii* Jennings. Ohio Natu ralist, 10 (5): 136.

Polytrichum strictum in Pennsylvania. Bryologist, 13: 100.

Notes on the distribution of certain plants in western Pennsylvania. Fern Bull., 1 (4): 99-101.

1911. Paleobotany. American Yearbook: 659-660.

The plant geography of the south shore of Lake Frie. (Abstract of paper read meeting) Ann. Assoc. Amer. Geographers, 1: 137-139.

Field-trip of the Botanical Society of Western Pennsylvania to Glenshaw, September 23, 1911. Bot. Soc. W. Pennsylvania Publ. 1: 5-9. (With John Bright)

Abstracts of the minutes of the Society [Bot. Soc. of W. Pennsylvania] for the year 1910-11. Bot. Soc. of W. Pennsylvania Publ. 1: 22-29.

A brief history of the Botanical Society of Western Pennsylvania. Bot. Soc. of W. Pennsylvania Publ. 1: 30.

Notes on the ferns of the Isle of Pines, West Indies. Amer. Fern Jour., 1 (6): 129-136.

1912. Some rare Ohio plants from Ashtabula County, Ohio. Torreya, 12 (5): 107-110, 1 fig.

Henry H. Negley [Obituary]. Bot. Soc. of W. Pennsylvania Publ. 2: 3, pl.

Shorter botanical notes. Bot. Soc. of W. Pennsylvania Publ. 2: 19-23.

Abstracts of the minutes for the year 1911-12 [Bot. Soc. of W. Pennsylvania]. Bot. Soc. of W. Pennsylvania Publ. 2: 23-30.

A note on the northwestern distribution of the sugar maple. Ottawa Naturalist, 26: 117-118.

1913. A manual of the mosses of western Pennsylvania. Publ. by the author, City Mission Publ. Co., Pittsburgh, Pa.: 1-429, 54 pl. of about 2300 detail figs. drawn by author.

Notes on the Pteridophytes of the north shore of Lake Superior. Amer. Fern Jour., 3 (2): 38-48.

Brachythecium pacificum, new species. Bryologist, 16 (6): 95-96, 20 figs. [in fig. 1].

Notes on the geology of the Isle of Pines, Cuba. Jour. Geology, 21 (4): 367-369.

Editorial [note]. Bryologist, 16 (3): 48.

1914. Henry Willey [biographical sketch]. Bryologist, 17: 75-76, 1 fig.

Notes on the Pteridophytes of the north shore of Lake Superior—II. Amer. Fern Jour., 4 (2): 68-73.

Publications of the Ohio Biological Survey. [Review of "Catalog of Ohio vascular plants," by J. H. Schaffner, and "A botanical survey of the Sugar Grove region," by Robert F. Griggs] Ohio Naturalist, 15 (1): 374-375.

915. Mossworts in Bessey's college botany. Bryologist, 18 (2): 30-31.

Bryology of New Zealand. [Comments on H. N. Dixon's "Studies on the bryology of New Zealand"] Bryologist, 18 (2): 31-32.

Notes on the life-history of *Sphagnum subsecundum.* Bryologist 18 (4): 63.

Short notes and reviews of current bryological literature. Bryologist, 18 (4): 63, 64, 80.

Systematic and ecological notes on the mosses of western Pennsylvania. Bryologist, 18 (6): 83-93, 1 pl.

Notes on the Pteridophytes of northwestern Ontario. Amer. Fern Jour., 5 (2): 33-39.

Illick's Pennsylvania trees [Review of "Pennsylvania trees" by J. S. Illick] Torreya, 15 (5): 109-112.

916. Nichols' vegetation of Connecticut [Review]. Bryologist, 19 (3): 49-50.

Short notes and reviews of current bryological literature. Bryologist, 19 (5): 79, 80, 81.

Odor of Conocephalus. Bryologist, 19 (5): 86.

Extracts from recent reports of "The Moss Exchange Club." Bryologist, 19 (6): 90-94.

Botanical reminiscences of the 1914 trip [by Bot. Soc. of W. Pennsylvania] to Pymatuning Swamp. Trillia, 4: 25-29.

In memoriam [Wm. R. Hamilton, Geo. C. Kennedy, Ferdinand S. Koeller, Cara Reese]. Trillia, 4: 52-53.

Abstracts of the minutes of the Botanical Society of Western Pennsylvania for Nov. 1912 to Oct. 1916. Trillia, 4: 54-68.

How to know the mosses, by Elizabeth M. Dunham [Review]. Plant World, 19: 326-328.

1917. Miscellaneous notes. Bryologist, 20 (1): 14-16.

Cooked lichens for food. Bryologist, 20 (2): 32.

Four-lobed spore mother-cells in Catharinaea. Bryologist, 20 (4): 64-66.

Hermann Edward Hasse—lichenist [Obituary]. Bryologist, 20 (4): 66.

The vegetation of Connecticut, by George E. Nichols [Review of Part V]. Bryologist, 20 (4): 66-68.

Pterygophyllum acuminatum at Ohio Pyle [stet.], Pennsylvania. Bryologist, 20 (6): 100.

Miscellaneous notes. Bryologist, 20 (6): 101.

A contribution to the botany of the Isle of Pines, Cuba, based upon the specimens of plants from that island contained in the Herbarium of the Carnegie Museum under date of October, 1916. Ann. Carnegie Mus., 11 (1-2): 19-290, 23 pl.

1918. Notes on recent bryological literature. Bryologist, 21 (1): 17.

Hold the lens on your thumb. Bryologist, 21 (1): 17-18.

Notes on the mosses of northwestern Ontario. I. Sphagnum. Bryologist, 21 (5): 69-78, 1 pl., 1 map.

Certain organic substances assimilated by *Ceratodon purpureus*. Bryologist, 21 (6): 86.

Notes on recent bryological literature. Bryologist, 21 (6): 90-96.

An annotated list of the Pteridophytes of northwestern Ontario. Amer. Fern Jour., 8 (2): 38-50, 1 map, 1 fig.

An annotated list of the Pteridophytes of northwestern Ontario—II (Ophioglossales). Amer. Fern Jour., 8 (3): 76-88.

Medical note for the tropical collector. Mus. Zool., Univ. Michigan, Misc. Publ. No. 3: 89.

1919. *Potamogeton Vaseyi* in northeastern Ohio. Ohio Jour. Sci., 19 (6): 343.

Lycopodium complanatum var. *flabelliforme* with seven spikes. Amer. Fern Jour., 9 (4): 119.

A description of *Cypripedium passerinum*. Ann. Carnegie Mus., 12 (2-4): 343-345 1 pl.

Proceedings of the Baltimore meeting of the American Association for the Advancement of Science [Report of Secretary]. Science, new ser., 49 (1253): 11-15.

John Adolph Shafer [Obituary]. Trillia, 5: 3-7, 1 pl.

The hawthorns of western Pennsylvania: a key to the species and a list, with th known localities. Trillia, 5: 34-60.

The B. H. Patterson herbarium presented to the Carnegie Museum. Trillia, 5: 84

Botanical notes on a trip to Mont Alto, Franklin County, Pennsylvania. Trillia, 5 85-88.

Abstracts of the minutes of the Society [Bot. Soc. of W. Pennsylvania] for th period from November, 1915, to October, 1919. Trillia, 5: 89-105.

In memoriam [8 obituaries—James J. Booth, Mrs. Charles P. Trimble, Mrs. James R. Mellon, J. H. Permar, John W. Thomas, Martha F. Vance, Gladys Howe, and J. Ludewig Koethen Jr.] Trillia, 5: 106-107.

Cardot's collections ravaged. Bryologist, 22 (1): 11-12.

Notes on recent bryological literature. Bryologist, 22 (2): 17-20.

Mr. Moxley finds new lichens for southern California. [A misc. note] Bryologist, 22 (3): 29.

Miscellaneous notes. Bryologist, 22 (5): 73-76.

Miscellaneous notes. Bryologist, 22 (6): 89.

1920. Abstracts of botanical articles, mainly in Spanish periodicals. Bot. Abstracts, 3: 222, 279, 435-436.

New or noteworthy plants from northwestern Ontario. I. Jour. Washington Acad. Sciences, 10 (16): 453-460.

Impatiens pallida forma *speciosa* f. nov. Ohio Jour. Sci., 20 (6): 204.

The paper mulberry (Broussonetia) an "artillery plant." Torreya, 20 (3): 52-53.

Rarity of *Conopholis*. The Amer. Botanist, 26 (1): 29.

1921. Fossil plants from the beds of volcanic ash near Missoula, western Montana. Memoirs Carnegie Mus., 8 (2): 385-450, 12 pl.

Studies in the genus Lactuca in western Pennsylvania. Ann. Carnegie Mus., 13 (3-4): 440-446, 1 pl. [Issued Apr. 25, 1922.]

Have the streams of Long Island been deflected by the earth's rotation? Science, new ser., 55 (1420): 291.

National parks and monuments threatened. Bryologist, 24 (1): 10.

Hepatics of Iberia (Spain and Portugal). [Review of A. Casares-Gil: Flora Iberica. Briofitas, Primera Parte. Hepaticas.] Bryologist, 24 (2): 30-31.

Miscellaneous bryological notes. Bryologist, 24 (2): 31.

922. Amelanchier in western Pennsylvania. Trillia, 6: 21-25 [1921].

Abstracts of the minutes of the Society [Bot. Soc. of W. Pennsylvania] for the period from Oct., 1919, to Oct., 1921. Trillia, 6: 41-52.

Annual report of the secretary [Bot. Soc. of W. Pennsylvania]. Trillia, 6: 53-54.

Miscellaneous notes. Bryologist, 25 (6): 111.

World metric standardization. Bryologist, 25 (6): 111-112.

923. The blazing star in western Pennsylvania. Trillia, 7: 12.

John Wynne Jones. Trillia, 7: 1-2, 1 pl. (With Neil McCallum)

The relation of smoke, fumes, and dust to the vegetation of the industrial district of Pittsburgh. Trillia, 7: 27-38.

Abstracts of the minutes of the Society [Bot. Soc. of W. Pennsylvania] for the period from Nov., 1921, to Oct., 1923. Trillia, 7: 39-52.

Necrology [Jennie Gosser, Francis Z. Schellenberg, and Andrew Vance]. Trillia, 7: 53-54.

Lichens crowd out mosses. Bryologist, 26 (1): 4. [Note on writing by McWhorter (Bot. Gazette, 72: 321-25, 1921) concerning subject]

Elias Judah Durand [Obituary]. Bryologist, 26 (6): 67.

)24. Pennsylvania trees, 4th ed., by Joseph S. Illick [Review]. Torreya, 24 (3): 52-54.

A study of an ecological succession of bryophytes and lichens on trees. [Review of Winfield Dudgeon, "Succession of epiphytes in the *Quercus incana* forest of Landour, western Himalayas." Preliminary note] Bryologist, 27 (3): 52-53.

How plants protect themselves in winter. The Scholastic, 4: 10, 28; 1 photo.

1925. Some inter-relations of birds and plants. The Cardinal, July (6): 1-5.

Some flowers and flower parts of angiosperms or flowering plants. Carnegie Mus. Botany Leaflet No. 1, 4 pp., illus.

Mosses with a hand-lens, by A. J. Grout [Review]. Bryologist, 28 (3): 40-42.

Methods of descriptive systematic botany, by A. S. Hitchcock [Review]. Bryologist, 28 (3): 69-70.

Topographical description of the Nawakwa Lodge environment. Trillia, 8: 1-4, 1 chart.

The white snakeroot: a plant poisonous to livestock and to man. Trillia, 8: 40-44.

Proceedings of the Botanical Society of Western Pennsylvania from Nov. 1923 to October 1925. Trillia, 8: 58-73.

Necrology [Miss Sophia C. Reineke, Mr. Neil McCallum, Mr. W. Lucian Scaife, and Mr. Henry Gibson]. Trillia, 8: 74-76.

1926. Summer school at Lake Erie (with Samuel H. Williams). Univ. of Pittsburgh Record, 1 (1): 20-26, 4 photos.

Notes on bryological literature. Bryologist, 29 (6): 74-77.

1927. The amateur gardener. [Three articles, one every other week in the Pittsburgh Gazette Times: Preparation of the soil, April 10; Some whys and wherefores of sowing and transplanting, April 24; The care of the garden, May 8]

The naturalist afield (with Samuel H. Williams). [A series of 10 radio talks on spring, talks 1, 3, 6, and 9 by Jennings: (1) The awakening of spring, pp. 5-15; (3) April flowers, the outburst of spring, pp. 26-35; (6) May—the greatest flower show of all, pp. 55-64; (9) the flowers of summer, pp. 85-94] Radio Publ. 30, Univ. of Pittsburgh.

The spring awakening of plants. Nawakwa Fireside, 1 (2): 2-4.

Loeske, L. Der Einfluss des Wassers auf Papillen und Mamillen, 1926. (The influence of water on Papillae and Mamillae) [Review]. Bryologist, 30 (5): 95.

Classification of the plant societies of central and western Pennsylvania. [Presidential address at 1925 meeting] Proc. Pennsylvania Acad. Sci., 1: 23-55, 5 pl., 1 map.

The range-limits and migrations of certain plants in western Pennsylvania [Abstract]. Proc. Pennsylvania Acad. Sci., 1: 105.

The John D. Shafer Herbarium. Bull. Carnegie Inst., 1 (4): 19-20, 2 photos.

Soil conditions and plant growth [Review], by E. J. Russell. Bull. Garden Club of Amer., no. 17, series 3: 48-51.

1928. Flowers for children: shall we plant for picking? Nawakwa Fireside, 3 (2): 2-4.

Common wild flowers of Pennsylvania, by Ernest M. Gress [Review]. Torreya, 28 (4): 71-78.

The flora of Cook Forest, Clarion and Forest counties, Pennsylvania. The Cardinal, 2 (3): 53-61.

The ancestry of mosses. Bryologist, 31 (1): 10-15.

Die Laubmoose Europas—the mosses of Europe, by Wilhelm Mönkemeyer [Review]. Bryologist, 31 (2): 37-40.

Miscellaneous notes on bryological literature. Bryologist, 31 (3): 62-63.

Pittsburgh—ninety million years ago. Carnegie Mag., 2 (2): 41-43, 2 photos.

April on the hillsides. The Pittsburgh Record, 2 (3): 198-205, 5 photos.

The growth of Presque Isle, Pennsylvania, and recent changes in its vegetation [Abstract]. Proc. Pennsylvania Acad. Sci., 2: 25-26.

The plant biography of a ravine in the Pittsburgh district. Proc. Pennsylvania Acad. Sci., 2: 100-101.

929. Plants for the home. Talk 9, Science for the home manager [Series of 14 radio talks]. Univ. of Pittsburgh Radio Publ. No. 48: 76-88.

Trees and flowers of spring: a series of eight radio talks broadcast from the University of Pittsburgh studio of KDKA, Pittsburgh. Univ. of Pittsburgh Radio Publ. No. 52, pp. 1-100.

Further notes on the plant geography of western Pennsylvania (Abstract). Proc. Pennsylvania Acad. Sci., 3: 42.

Homalocenchrus virginicus, a sensitive grass. Proc. Pennsylvania Acad. Sci., 3: 43.

The Arizona desert group. Carnegie Mag., 3 (7): 215-216.

Notes on bryological literature. Bryologist, 32 (1): 15-20.

Notes on bryological literature. Bryologist, 32 (3): 66-67.

Checklist of pleurocarpous mosses [Review]. Bryologist, 32 (6): 115.

930. A state flower for Pennsylvania. The Pittsburgh Record, 4 (4): 56-59, 1 fig.

Abstracts of the minutes of the Botanical Society of Western Pennsylvania, for the period from Oct., 1925, to Sept., 1930. Trillia, 9: 70-90.

Necrology [Geo. H. Burke, J. D. Shafer, A. E. Ortmann, A. E. McKee, Chas. L. Abbott, Sarah B. Rankin, Wm. Falconer, G. H. Rankin, Elizabeth G. Milliron, Geo. B. Parker, Allen Davis, Frank Read Alker, Cadwallader W. Parker, Margaret J. Vance]. Trillia, 9: 91-98, 1 photo.

Moss distribution in the eastern United States, by George B. Kaiser [Review]. Bryologist, 33 (6): 77.

Annales Bryologici [Review]. Bryologist, 33 (4): 55-56.

Die Laubmoose Europas, II—Funariaceae, by Leopold Loeske [Review]. Bryologist, 33 (5): 69-70.

Peregrinating Presque Isle. Carnegie Mag., 4 (6): 171-175, 5 photos., 1 fig.

A survey of the phytoplankton at Erie, Pennsylvania. Science, 71 (1848): 560-561.

Bird notes from Presque Isle. The Cardinal, 2 (7): 181-185, 1 map.

Brief notes on the natural history of the Erie [Pa.] region [Publ. with the program for field meeting of the Pennsylvania Acad. Sci., Erie, Pa., Aug. 1-2, 1930]. 1 map. (With S. H. Williams and H. Leighton.)

Areas of biological interest in western Pennsylvania deserving preservation. Proc. Pennsylvania Acad. Sci., 4: 30-32.

31. Exsiccatae: *Bryotheca gallica*. Bryologist, 34 (1): 7-8.

Notes on bryological literature. Bryologist, 34 (5): 76.

Recent literature on bryophytes and lichens. Bryologist, 34 (6): 94-96.

32. Our State tree. Pittsburgh School Bull., Jan.: 172. [From an editorial, Pittsburgh Post-Gazette.]

The Florida jungle group. Carnegie Mag., 6 (3): 75-77, 1 photo.

Autumn colorings. Carnegie Mag., 6 (6): 174-176, 2 photos.

Book review. Manual of bryology. Bryologist, 35 (4-6): 86-87.

Book review. Moss flora of North America. Bryologist, 35 (4-6): 88.

Description [In "A new Hydrocotyle from western New York," by Edith Fetherston] of *Hydrocotyle fetherstoniana* Jennings, sp. nov. Torreya, 32: 6-8.

Where is Nawakwa? Nawakwa Fireside, new ser., 1: 3-5.

1933. The Jacob Wolle Herbarium. Carnegie Mag., 7 (2): 50-51.

The passing of Pymatuning Swamp. Carnegie Mag., 7 (7): 202-207, 1 fig., 5 photos.

Limnological studies at Erie, Pennsylvania. Trans. Amer. Microscopical Soc., 52 (3): 181-191, 4 fig. (With R. Y. Gottschall)

Some interrelations of plants and birds on Presque Isle, Erie, Pennsylvania. Proc. Pennsylvania Acad. Sci., 7: 192-195.

Book review. Annales bryologici. Bryologist, 36 (1-4): 43.

Miscellaneous shorter reviews. Bryologist, 36 (1-4): 44.

Editorial notes. Bryologist, 36 (1-4): 48.

1934. The nomenclature of some of the mosses of the species Muscorum. Bryologist, 37 (3): 63-64.

North American Musci perfecti. Bryologist, 37 (6): 105-106.

Field work with the cryptogams, its needs and methods. Bull. Torrey Bot. Club, 61: 89-92.

Smoke injury to shade trees. Proc. 10th Natl. Shade Tree Conference, Pittsburgh, Pa., Aug. 30-31: 44-48.

The Mount Rainier group. Carnegie Mag., 7 (8): 243-244, 2 photos (one scene, on cover, and one of O. E. Jennings).

1935. Ecology in museum exhibition. Museum News, Dec. 15: 8. [From a paper read at annual meeting, Amer. Assoc. of Museums at Toronto, May 30-June 1, 1934]

Check list of mosses of western Pennsylvania. [Included in the manual of mosses of western Pennsylvania and privately published as a booklet, pp. 1-17.]

A new method of mounting moss dissections in Canada balsam. Bryologist, 38 (2): 29-30.

Desmatodon arenaceus versus *Tortula obtusifolia*. Bryologist, 38 (3): 60.

1936. Bryophyta (bryophytes) of Southampton Island. Memoirs, Carnegie Mus., 12: 7-16, figs. 1-19.

Algae and fungi of Southampton Island. Memoirs, Carnegie Mus., 12, pt. 3: 343-345, 1 pl.

Moss flora of North America north of Mexico, by A. J. Grout [Review]. Bryologist, 39 (2): 24.

1937. The Pennsylvania bog group. Carnegie Mag., 11 (3): 86-88, 2 photos (one of bog on cover and one of O. E. Jennings).

Plants characteristic of Christmas. Carnegie Mag., 11 (7): 195-196, 4 figs.

Fink's lichen flora of the United States [Review]. Bryologist, 40 (3): 64.

1939. Berkey Hunter Patterson. Trillia, 10: 17-18, 1 photo.

A contribution towards a plant geography of western Pennsylvania. Trillia, 10: 46-81, 6 pl.

Abstracts of the minutes of the Botanical Society of Western Pennsylvania, Oct. 1930 to Oct. 1936. Trillia, 10: 102-132.

Necrology. Trillia, 10: 137-139.

1940. John and William Bartram, botanists and explorers, 1699-1777, 1739-1823, by Ernest Earnest [Review]. The Western Pennsylvania Historical Mag., Dec., 1940: 258-260.

1941. Spring wildflowers. Carnegie Mag., 15 (1): 3-8, 9 photos.

1942. The verticillate Eupatoriums of western Pennsylvania. Castanea, 7 (3): 43-48.

A Pittsburgh botanist afield. Carnegie Mag., 16 (2): 49-55, 10 photos.

1943. The ecological plant geography of western Pennsylvania. Quarterly Bull. Polish Inst. of Arts and Sciences in Amer., July: 1-16, 2 figs.

1944. Ecological plant geography of western Pennsylvania as related to bird life. The Ruffed Grouse, no. 1: 10-15.

1945. Range of *Mnium hornum*. Bryologist, 48 (3): 158.

Edaphosaurus—a finback reptile. Carnegie Mag., 19 (3): 67-68, 2 photos.

Woodland path. Carnegie Mag., 19 (4): 108, 1 photo.

Woodland path. Carnegie Mag., 19 (5): 148, 1 photo.

Woodland path. Carnegie Mag., 19 (6): 183, 1 photo.

946. Woodland path. Carnegie Mag., 19 (7): 211.

Woodland path. Carnegie Mag., 19 (8): 245, 1 photo.

Woodland path. Carnegie Mag., 19 (9): 269, 1 photo.

Woodland path. Carnegie Mag., 20 (1): 15, 1 photo.

Woodland path. Carnegie Mag., 20 (2): 48, 1 photo.

Woodland path. Carnegie Mag., 20 (3): 84, 1 photo.

Out of doors. Carnegie Mag., 20 (4): 122, 1 fig.

Out of doors. Carnegie Mag., 20 (5): 153, 1 fig.

Out-of-door decorations. Carnegie Mag., 20 (6): 176-177, 4 figs.

947. Why ignore chlorophyll? Carnegie Mag., 20 (7): 208-209.

Out of doors. Carnegie Mag., 20 (7): 215, 6 figs.

Out of doors. Carnegie Mag., 20 (8): 246, 1 fig.

Out of doors. Carnegie Mag., 20 (9): 274, 1 fig.

Out of doors. Carnegie Mag., 20 (10): 299, 1 fig.

Out of doors. Carnegie Mag., 21 (1): 21, 1 fig.

Out of doors. Carnegie Mag., 21 (2): 42, 1 fig.

Jack-in-the-pulpit. Carnegie Mag., 21 (2): 34, cover illus.

A gift of flower paintings. Carnegie Mag., 21 (2): 41-42.

Tree of the month [black gum]. Carnegie Mag., 21 (3): 79, 1 fig.

Tree of the month [scarlet oak]. Carnegie Mag., 21 (4): 111, 1 fig.

The campus. Pitt, summer issue: 3-5. 6 photos.

Choosing your Christmas tree. Carnegie Mag., 21 (5): 144-145, 4 figs.

A new variety of *Gentiana Saponaria* [var. *allegheniensis*]. Castanea, 12 (1): 57-58.

948. Plant life of western and central Pennsylvania. Pennsylvania Game News, Jan.: 10, 27-28.

McConnell's Mills; Pymatuning Swamp region; Presque Isle; Cook Forest State Park; Ohio Pyle; The Grand Canyon of Pennsylvania. Western Pennsylvania Highways and Byways for Gardeners, prepared by the Western Region of the Garden Club Federation of Pennsylvania. 32 pp.

Tree of the month [pine]. Carnegie Mag., 21 (6): 181, 2 figs.

Tree of the month [sugar maple]. Carnegie Mag., 21 (7): 207, 1 fig.

Tree of the month [ash]. Carnegie Mag., 21 (8): 232, 1 fig.

Tree of the month [shadblow]. Carnegie Mag., 21 (9): 265, 1 fig.

Tree of the month [redbud]. Carnegie Mag., 21 (10): 305, 1 fig.

Wild flower guide: northeastern and midland United States, by Edgar T. Wherry [Review]. Carnegie Mag., 21 (10): 315-316, 1 photo.

Tree of the month [tulip]. Carnegie Mag., 22 (1): 14, 1 fig.

Tree of the month [*Rhododendron maximum*]. Carnegie Mag., 22 (2): 45, 1 fig.

The sciences in Pittsburgh, II. Botany. Carnegie Mag., 22 (4): 125-128, 4 photos.

The shifting sands of Presque. Pennsylvania Park News, 59: 6-7, 11.

1949. Nature's finishing touches. Carnegie Mag., 23 (2): 54-57, 7 figs.

1951. Rare or less commonly collected plants of western Pennsylvania. Trillia, 11: 146-163.

A manual of the mosses of western Pennsylvania and adjacent regions, 2nd ed. Univ. Notre Dame Press, Notre Dame, Ind., pp. 1-396, 72 pl., 1 map.

Warren R. Witz (Obituary). Castanea, 16 (4): 142-143.

The rose, queen of flowers. Carnegie Mag., 25 (6): 192-193, 2 figs.

Consider the lilies. Carnegie Mag., 25 (8): 269-271, 2 photos.

Orchids. [Note on presentation to Carnegie Institute of 4 vols. of *Reichenbachia*, by Mrs. Howard Heinz.] Carnegie Mag., 25 (8): 282.

1952. Edmund W. Arthur as a botanist. The Ruffled Grouse, no. 3: 6-7.

Eupatorium sessilifolium f. *inciso-serratum* f. nov. Castanea, 17 (3): 138.

1953. Is it good to eat? Carnegie Mag., 27 (8): 273-275, 3 figs.

A range-extension for sugar maple. Rhodora, 55: 59.

Wild flowers of western Pennsylvania and the Upper Ohio Basin, 2 vols. Univ of Pittsburgh Press, Pittsburgh, Pa. Vol. 1, 600 pp. text, incl. 146 range and distribution maps. Vol. 2, 200 colored plates, illus. 253 plants, by Andrey Avinoff, with descriptions by O. E. Jennings.

Nature's autumn show. Pitt, no. 48: 31.

1954. Scholars. Pitt, no. 52: 30-31, 1 photo.

How some plants avoid winter-killing. The American Biology Teacher, 16 (5): 111 112.

1955. Ecology in this changing world. Carnegie Mag., 29 (1): 15-18, 2 photos.

Our national flower. Carnegie Mag., 29 (2): 44.

An office favorite [*Haemanthus katherinae*]. Horticulture, 33: 560.

1956. The Englishman's flora, by Geoffrey Grigson [Review]. Bull. Garden Club o Amer., 44 (6): 32-34.

The Pittsburgh weed. Carnegie Mag., 30 (6): 203, 1 fig.

1957. Spring is just around the corner. Carnegie Mag., 31 (3): 89.

Cook Forest Park. Carnegie Mag., 31 (4): 116-119.

This summer's drought. Carnegie Mag., 31 (8): 263-264, 274. (With Harry K Clench)

1958. *Thelepogon elegans* Roth in the Dominican Republic. Rhodora, 60: 73.

When Pittsburgh was a lake. Carnegie Mag., 32 (2): 48-50, 68, 2 figs.

How was it formed? [*In* "The story of Presque Isle, Pennsylvania"] Dept. of Forests and Waters, Harrisburg: 8-13.

Charleston, S.C., hospitality. Carnegie Mag., 32 (6): 207-209.

Trillium in the woods. Printed on fold-sheet, with "The traveller and the trillium by Edwin L. Peterson, and distributed with note paper displaying trillium flower Bicent. Comm., Fox Chapel Garden Club, Pittsburgh, Pa.

1959. Ferncliff, a botanist's paradise. Water Land and Life, 1 (1): 5-6.

Forest resurgent at Ohiopyle. Water Land and Life, 1 (2): 12-15.

Greatest natural color show on earth. Water Land and Life, 1 (4): 11-13.

Darwin and his theory. Carnegie Mag., 33 (10): 349-353, 2 photos.

Succession: a unique case history. Landscape Architecture, 49 (4): 235-236, 1 fig., 1 photo.

1960. Presque Isle's last stand. Water Land and Life, 2 (1): 8-10, 15, 4 figs.

1961. Biological control of pests. Carnegie Mag., 35 (6): 209-213.

Fruit-bearing plants and birds. Audubon Mag., 63 (5): 281-285.

Cucumber [Run] Valley flora rich in interest. Water Land and Life, 3 (3): 12, 15.

1962. Trees are interesting. Carnegie Mag., 36 (8): 263-266.

Trees and shrubs of Ferncliff Park. W. Pennsylvania Conservancy Pocket Guide No. 2, 10 pp., May.

1963. What will happen to our white oaks? Water Land and Life, 5 (2): 19-20.

Silent spring, by Rachel L. Carson [Review]. Carnegie Mag., 37 (4): 137-141.

Throngs hear blazing star romance [Address delivered at Jennings Blazing Star Prairie, Aug. 11, 1963]. Water Land and Life, 5 (3): 27-30.

Scholar tree. Carnegie Mag., 37 (7): 231.

1964. John Bright, 1872-1952. Trillia, 12: viii-x, 1 photo.

List of evening programs [Bot. Soc. of W. Pennsylvania], Oct., 1946, to Sept., 1963. Trillia, 12: 134-146.

List of field trips [Bot. Soc. of W. Pennsylvania], Oct., 1946, to Sept., 1963. Trillia, 12: 147-159.

1965. Trees and shrubs of Ferncliff Park, W. Pennsylvania Conservancy Pocket Guide No. 2, rev. ed., 20 pp., Jan.

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ANNALS
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OLUME 44 MAY 10, 1973 ARTICLE 7

FOSSIL FISHES FROM SOUTHWESTERN PENNSYLVANIA, ART II: *MONONGAHELA DUNKARDENSIS*, NEW SPECIES, IPNOI, LEPIDOSIRENIDAE) FROM THE DUNKARD GROUP

Richard Lund[1]
Research Associate, Section of Vertebrate Fossils

Introduction

Study of the fresh water limestones of the Late Pennsylvanian and
rly Permian of southwestern Pennsylvania reveals that dipnoans
nstituted an important part of the fish fauna during that time.
rge fragmentary specimens of *Sagenodus* cf. *S. periprion*, as well as
jaws of postlarval individuals, occur with great regularity through-
t the local geologic column. Occasional specimens of *Monongahela*
nodonta (Lund, 1970b) have been found from the Upper Freeport
nestone of the Upper Allegheny Group through the Lower Washing-
Limestones of the Dunkard Group. A second species of the genus
nongahela, described below, has been found only in the Washington
Greene Formations, but in astonishing concentrations. The hun-
ds of jaws of this species that can be extricated from individual sedi-
ntary layers permit intensive statistical investigation into evolution-
trends within the species and into the details of species formation
he genus *Monongahela*.

This study was initiated under a grant by the Pittsburgh Foundation.
drawings and graphs were executed by Miss A. Lee Ambrose. The
cimens are deposited in Carnegie Museum (CM), Section of Verte-
te Fossils.

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partment of Earth and Planetary Sciences, University of Pittsburgh, Pittsburgh, Pa.
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NATURAL HISTORY SURVEY
MAY 17 1973
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TECHNIQUES

The extraction of large numbers of matrix-free lungfish jaws from fresh-water limestones with a high silt content proved quite difficult using established methods of acid preparation. The small size of many of the specimens made the development of a better technique imperative. Discovery of the usefulness of Amine-220 plus methyl amyl alcohol (Lund 1970a) fortunately supplied part of the answer to the problem. Further refinement of the techniques of chemical preparation using these compounds plus other chemicals has proven invaluable in a great variety of preparation problems. A brief discussion of the various techniques will be helpful in many paleontologic applications.

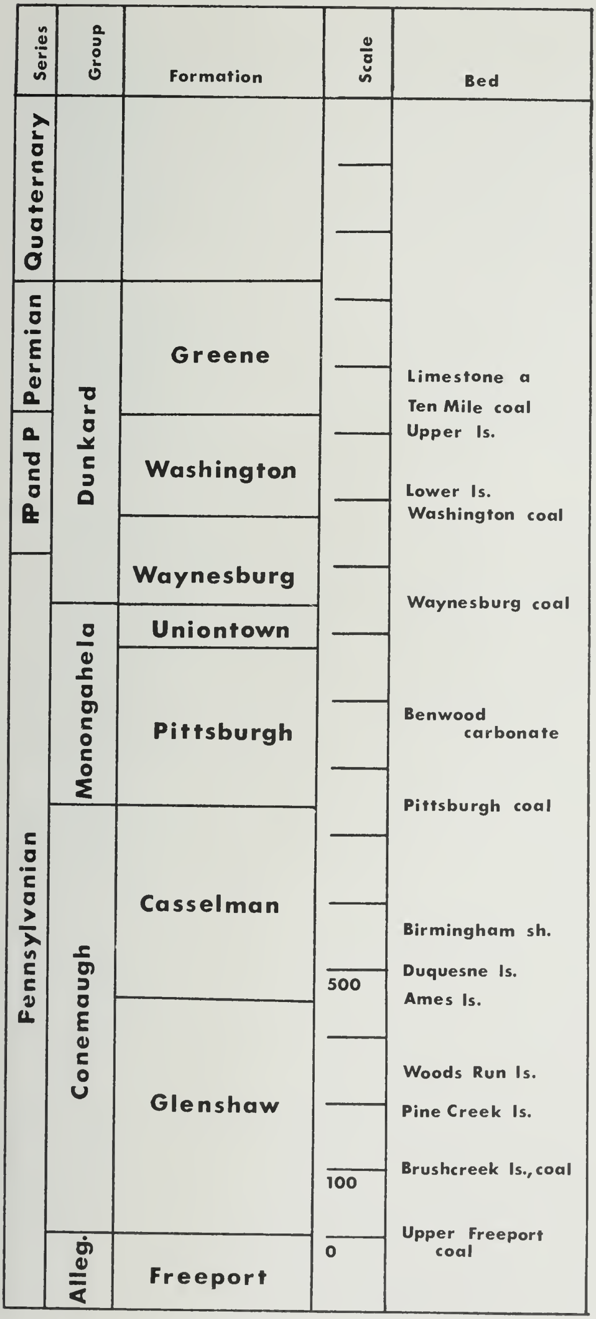
Amine-220 is an alkanolamine manufactured by the Union Carbide Corporation. In combination with other chemicals, it is capable of separating silt and clay sediment particles from each other in a manner apparently similar to, but considerably more effective than that of a detergent. The action of Amine-220 in water is quite limited. The addition of 1% Amine-220 to 10% formic acid greatly aids in preventing silt buildup on the surface of blocks of high-silt limestones. Stronger solutions of formic acid, up to 15%, combined with Amine-220 have been used to break down sandstones with calcareous cement, for example, the Como Bluff, Wyoming, Jurassic Morrison Sands. Formic acid without Amine-220 only seems to replace the surface layer of calcareous cement with a complex crystalline acid residue. With 1% Amine-220 in ½%-¼% acetic acid it is now possible to etch calcareous foraminifera and scaphopods from siltier phases of the Ames (Upper Pennsylvanian) Limestones of the Pittsburgh region.

Ammonium oxalate in Amine-220 solution is very effective in removing rust from large and small bones and invertebrates, a reaction that is speeded by sunlight. Acidified solutions of this combination are effective in the case of complex rusty deposits found on mine-dump coal shales, like the cannel shales of Linton, Ohio.

Methyl amyl alcohol is an exceedingly effective vehicle for Amine-220 in silts and shales. This combination is used to treat acid residues in order to concentrate as well as to clean the bone (Lund, 1970a). Brushing this solution onto matrix over fossils in paper shales, followed by careful removal with a very soft, short-haired brush, has made it possible to prepare very small syncarid crustacean fossils from the Mississippian of Montana.

While Amine-220 is not a cure-all in chemical preparation problems, it does help in a number of ways. Occasions arise, however, when one is reminded that simple chemicals like commercial washing soda should always be tried first.

Fig. 1. Generalized geologic column for southwestern Pennsylvania (after Berryhill, 1963)


Series
Group
Formation
Scale
Bed
Quaternary
Permian
ℙ and P
Pennsylvanian
Dunkard
Monongahela
Conemaugh
Alleg.
Greene
Washington
Waynesburg
Uniontown
Pittsburgh
Casselman
Glenshaw
Freeport
500
100
0
Limestone a
Ten Mile coal
Upper ls.
Lower ls.
Washington coal
Waynesburg coal
Benwood carbonate
Pittsburgh coal
Birmingham sh.
Duquesne ls.
Ames ls.
Woods Run ls.
Pine Creek ls.
Brushcreek ls., coal
Upper Freeport coal

MEASUREMENTS

Angular measurements were made with a goniometer mounted on the left ocular of a binocular microscope, at 16x magnification. The goniometer was made at a cost of 59¢ from a plastic protractor and two hose clamps, according to the design of Smith (1956). Measurement of the angles is accurate to within ½ degree. Statistical parameters were calculated by computer. Specimens were positioned for measurement in 4-well foraminifera slides (W. H. Curtin Co.) using gum tragacanth.

PHOTOGRAPHS

Photographs were taken by scanning electron microscope, using Polaroid P-N 55 film. The S.E.M. was manufactured by, and the photography supported in part by, the Ultrascan Corporation. The photographs were taken through the courtesy of Richard Matta, Department of Radiology, Presbyterian-University Hospital, University of Pittsburgh.

Geologic Setting

CORRELATION

Upper Pennsylvanian and Lower Permian sedimentary rocks of western Pennsylvania that have yielded lungfish of the genus *Monongahela* range from the Freeport Formation, Allegheny Group, through to the base of the Greene Formation, Dunkard Group (Fig. 1). The oldest known specimen is a single large pterygoid of *Monongahela stenodonta* from the Upper Freeport Limestone of Linton, Jefferson County, Ohio. This formation correlates with the Missourian of the Midcontinent section (Sturgeon and Hoare, 1968) and with the late Westphalian D of the European section (Baird, 1962).

Specimens of *Monongahela stenodonta* from the Duquesne Limestones (Casselman Fm., Conemaugh Group) (Lund, 1970b) are found about 50 feet above the Ames Limestone. Sturgeon and Hoare (1968) assign a Virgilian age (equivalent to Stephanian of the European section; Darrah, 1935), to the Ames Limestone, the last major marine tongue in western Pennsylvania. Fragmentary remains assigned to *M. stenodonta* are found in the Lower Pittsburgh Limestones of the old Soho Street Quarry, Herron Hill, Pittsburgh (Moran, 1952). These limestones, 40 feet from the top of the Casselman Formation, are considered also to be Virgilian in age.

The youngest fossils assignable to *M. stenodonta* are from a very thin limestone at the top of the Lower Washington Limestones, Washington Formation, Dunkard Group, of Washington, Pennsylvania.

Correlation of Dunkard Group rocks, based principally on floral evidence, is given as basal Permian (Wolfcampian, Autunian) by Berryhill (1963). Darrah (1935), on the basis of the first occurrence of *Callipteris conferta*, placed the Pennsylvanian-Permian boundary at the top of the Washington Formation. Clendening (1969), on the basis of fossil pollen and spores from Appalachian basin and "selected" Kansas sections, placed the entire Dunkard Group in the Virgilian (Pennsylvanian). Peppers, (1964), after a detailed analysis of spores from Illinois coal basins, indicates that time correlations based on spores are exceedingly uncertain for several reasons, one of which is that spores are easily reworked from older clastic deposits.

In view of the difficulties Peppers ėncountered within coal basins in Illinois, the work of Clendening (1969), comparing selected sections from Kansas and Pennsylvania-West Virginia, seems to be on very dubious conceptual grounds, although perhaps no more dubious than relying on the first occurrence of one species of plant, *Callipteris conferta.* Little help is found in attempting to correlate from the Permian type section in Russia, although there are indications that the base of the recognized Russian Permian may fall at a level higher than that of the youngest Dunkard rocks (Romer, 1952).

The oldest recognizable jaws of the second species of *Monongahela* are found in the Lower Washington Limestone, in the same rocks as those of *M. stenodonta.* They are distinct from the latter species, and are there quite rare. Large populations of the second species occur throughout a 22-foot section of Upper Washington Limestones and in ostracod limestone lenses four feet above the top of the Upper Washington Limestone, in the Greene Formation. The numbers of specimens in each limestone layer in a quarry at Vance, Washington County, Pennsylvania (Arkle, 1959) were so high that for purposes of analysis only samples from the uppermost and lowermost layers have been considered in this paper. The age of the rocks is apparently somewhere near the Pennsylvanian-Permian boundary. There are no younger representatives of either species presently known in the Appalachian basin.

SEDIMENTARY ENVIRONMENT

Sediments of the Appalachian basin of the late Allegheny and Conemaugh Groups are characterized by rhythmic lithologic variation representing every environment from terrestrial to offshore marine. Studies of the environments of deposition of individual sedimentary cycles usually reveal complex coastal plain and deltaic facies (Williams, et al, 1964; Morris, 1968).

Broadly, the nature of the cyclical deposits changes from fluctuating transgressive-regressive near shore sediments to sediments lacking a transgressive sequence at the middle of the Conemaugh. The last marine transgression known in western Pennsylvania occurs at the top of the Birmingham cycle (Raymond, 1910) although brackish-water brachiopods occur at the level of the Washington Coal in southeastern Ohio. The Monongahela Group is characterized by very widespread fine carbonate layers, interbedded with clays, almost no other clastic material, and virtually no fossils or significant organic matter in the carbonates. The Uniontown and Waynesburg Formations resume cyclical sedimentation of a strictly non-marine nature, containing various clastic sediments and local fresh-water limestones, indicating a return to normal upper delta-plain environments. The Washington Formation contains, in addition to upper delta-plain environment features, Lower, Middle, and Upper fresh-water limestone members, each generally persistent but variable in thickness, numbers of layers, and composition. The Greene Formation contains cyclical clastics with occasional limestone lenses. The average thickness of the section from the base of the Conemaugh to the top of the Greene Formation in southwestern Pennsylvania is about 950 feet (Moran, 1952).

LOCAL OCCURRENCE OF FOSSIL LUNGFISH

Lungfish, e.g. adult *Sagenodus*, are found in a wide variety of sedimentary environments in local fresh-water coastal-plain sediments. *Sagenodus* has been reported from the cannel shales at Linton, Ohio (Newberry, 1875), from shales and clay shales in the Washington Formation near Marietta, Ohio (Romer, 1952), from various fresh-water limestones like the Duquesne Limestone (Lund, 1970b) and from fluviatile sandstones. Members of the genus *Monongahela* have been found chiefly in association with fresh-water limestones. There are no definite indications of lungfish burrows in the southwestern Pennsylvania section.

SYSTEMATICS

The Pennsylvanian lungfish, *Monongahela stenodonta,* known from isolated jaws (Lund, 1970b), is clearly related to *Gnathorhiza* from the Permian of Texas and Oklahoma (Berman, 1968; Carlson, 1968; Olsen 1951). Strong resemblances between *Gnathorhiza* and the modern

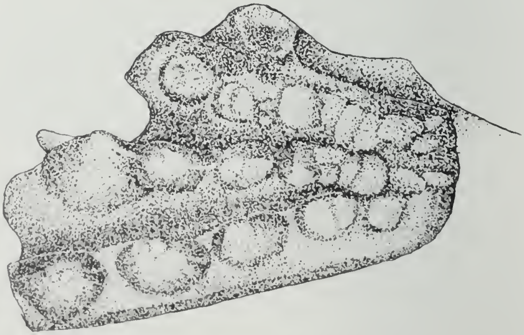


Fig. 2. *Monongahela dunkardensis,* left pterygoid plate, CM 24800, type.

Lepidosirenidae have led most authorities to classify these late Paleozoic fishes as Lepidosirenidae (Carlson, 1968). The cranial osteology of the Recent forms, however, is so highly modified that little practical comparison may be made at this time with any fossil form (Carlson, personal communication). Examination of evolutionary trends among the Paleozoic Dipnoi, particularly of forms supposedly allied to the lepidosirenids, may shed some new light on the problem. The discovery of large populations of a second species of *Monongahela* provides a good opportunity for a study of evolutionary trends and evolutionary potential in this group.

Order Dipnoi
Family Lepidosirenidae Bonaparte, 1841
Genus *Monongahela* Lund, 1970

REVISED DIAGNOSIS: Lungfish, related to *Gnathorhiza* and known only from toothed elements, recognizable on the basis of the following criteria: pterygoid element usually with four discrete tooth ridges, the anterior ridge parasymphysial, the first three ridges divergent from an apex, the most posterior ridge originating lateral to the apex and to the point of origin of the third ridge, palatal bone not extending under lateral ends of posterior three ridges; prearticular element usually with three tooth ridges divergent laterally, the anterior ridge longest and parasymphysial, the posterior ridge originating posterior to the apex of the other two ridges, the bone vertically developed, with a posterior coronoid enlargement.

TYPE SPECIES: *Monongahela stenodonta*, Lund, 1970

Monongahela dunkardensis, new species
Figures 2-4

HORIZON: An ostracodal sand lens 1 foot by 1 foot by 1½ inches thick, in a mudstone 4 feet above the top of the Upper Washington Limestone, Greene Formation, Dunkard Series, Wolfcampian?, Permian?

LOCALITY: Washington Stone Company Quarry at Vance, Washington County, Pennsylvania, latitude 40° 10′N., longitude 80° 11′W. Refer to United States Geological Survey Map GQ 334, 1964.

HOLOTYPE: Carnegie Museum 24800, left pterygoid tooth plate.

REFERRED SPECIMENS: Carnegie Museum numbers 24780-24799, 24801-24891, pterygoids; 24892-24899, 25100-25205, prearticulars.

DIAGNOSIS: Lungfish of the genus *Monongahela,* known only from jaw elements. Jaw elements with cusps of tooth ridges rounded, and central core flattened transverse to he axis of the tooth ridge. Cusps united in separate rows when young, with cusps and ows becoming fused and obscured from the apex outward with increased growth, to orm a heel. Cores of the cusps remain discrete. Pterygoid tooth plates with 4 tooth rows but a tendency to develop the most posterior row late in ontogeny or not at all. Prearticular with 3 tooth rows and a tendency to reduce the third (posterior) row to a mooth spur. Angles between pterygoid tooth ridges, from front to rear: AB, mean 4.37°, extremes, 7°, 28°; BC, mean, 15.49°, extremes, 9°, 32°. Angles between prearticular tooth ridges, front to rear: AB, mean 23.30°, extremes, 14°, 35°; BC, mean 26.96°, extremes, 14°, 75°. Both pterygoid and prearticular bones tend to thicken greatly at the symphysis with increased growth, pterygoid with prominent descending quadrate process, prearticular with well-developed coronoid process. No single-bladed prearticulars present. Jaws of extremely small size, largest known prearticular about 3 mm. in length.

GEOLOGIC RANGE

Lower Washington Limestones, Washington Formation, Dunkard Group, through to the base of the Greene Formation, Dunkard Group, Lowest Wolfcampian?, Permian?.

Monongahela jaws incorporating several of the features of *M. dunkardensis,* and distinguishable from typical *M. stenodonta,* can be recognized as early as lowest Virgilian, in the Duquesne Limestones. While the erection of a species boundary between two species is by nature arbitrary, significant numbers of individuals that probably represent separate or separating populations have yet to be found below the Lower Washington Limestones.

The quantitative data given in the diagnosis fit only the population at the upper limit of the presently known range of the species. Rapid rates of change in all characters make it impossible to present a diagnosis accurate for more than a single time plane. In the quarry at Vance, Pennsylvania, jaws of this lungfish have been found in each of the limestone beds comprising the upper 10 feet, in the siltstone and mudstone in contact with the top of the limestone sequence, and in the yellow silty limestones comprising the bottom seven or eight feet of the Upper Washington Limestones, behind an abandoned brickyard at the entrance to the quarry. Lungfish jaws from all horizons were collected and examined and the variation was found to be consistent throughout the section. Jaws from the uppermost and lowermost horizons in the quarry were selected for intensive analysis.

GENERAL MORPHOLOGY

The pterygoid of *M. dunkardensis* consists of a flat plate, longer than wide, with a long symphysis and a sharply downturned posterolateral corner or quadrate process. Three or four rows of teeth are found on a pterygoid plate, a parasymphysial row, row A; an anterolateral row, row B; a lateroanterior row, row C; and the last row to develop, row D (Fig. 16). Rows A, B, and C generally radiate from a projected common center of origin, and row D originates from the side of row C. Row D is not commonly present in younger individuals and contains very few cusps when it is present. Individual cusps in the tooth rows are short and conical.

The prearticular is a vertically developed bone, which meets its counterpart at an angle of about 90°. Three rows of cusps surmount the bone, a parasymphysial row, row A; an anterolateral row, Row B; and a lateroanterior row, row C. Row A is generally the longest, and row C the shortest. The three rows diverge from an actual, rather than a projected point. The cusps are conical and broad at the base. The coronoid process arises immediately behind the tooth platform.

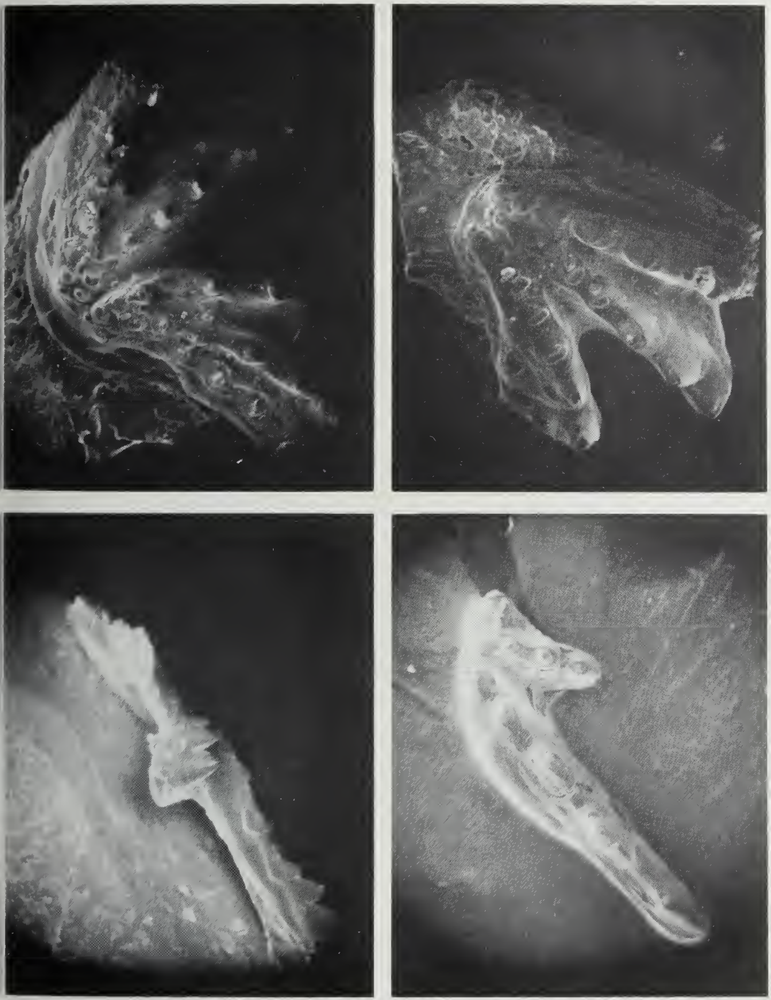


Fig. 3. *Monongahela*, pterygoids. Top left, *M. dunkardensis*, CM 24880; top right, CM 24705, Duquesne Limestone; lower right, Lower Washington Limestone No. 2.

Successive teeth in each row of both jaws are increasingly broad and increasingly distant from the next cusp proximally. Wear progresses from the proximal ends of rows B and C on both jaws, anterolaterally, soon involving row A as well. Growth of the teeth occurs from within as wear progresses externally, as shown by the observation that the proximal ends of the tooth rows are completely separate on the jaw in very small individuals, and very short, but merge and increase in height in larger individuals (fig. 3). Wear and growth combine to produce a flat heel incorporating the proximal ends of the first three rows of the upper jaw and spreading laterally with age. A central core of non-tubular dentine, oriented transverse to the tooth row, is present in each tooth. This resistant column is exposed by wear, and as the tooth ridges merge into a heel the cores are left standing slightly above the surface of the heel. The cores of the teeth thus provide a textured grinding surface.

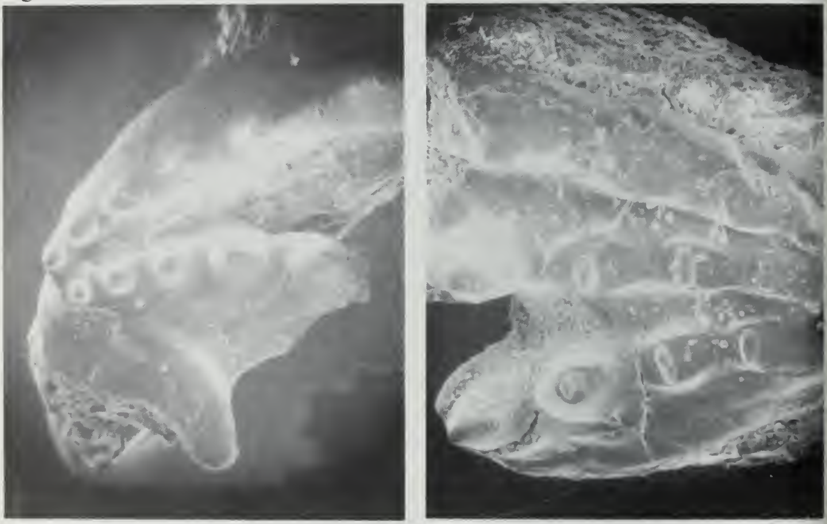


Fig. 4. *Monongahela dunkardensis*, prearticulars. Left, CM 25143; right, uncatalogued specimen.

Resistant central cores are present in *M. stenodonta* that seem to be round or elongated slightly along the axis of the row. In *Gnathorhiza dikeloda* from the Leuders Formation (Olson, 1951), columnar centra cores present in the teeth of young individuals are supplemented by additional columns of dentine between the original cores with increased size. In apparently adult individuals, a single ridge of dentine runs the length of each tooth row. In horizontal ground sections examined unde the petrographic microscope, the crystallographic integrity of each column can be observed.

OCCLUSION

There is no shearing action of tooth rows of opposing jaws in *M. dunkardensis,* as there is in *M. stenodonta* (Lund, 1970b) or in *Gnathorhiza serrata* (Berman, 1968: 831). The relationship between upper and lower jaws produces a flat grinding heel upon the palate, where there is no good indication of the direction of jaw motion or of relative tooth row position.

VARIATION AND GROWTH

Quantitative studies of growth and variation of jaws of the genus *Monongahela* were based upon two sets of factors, the number of cusps in tooth rows, and the angles between tooth rows. Studies of cusp numbers are directly related to growth stage, as cusps are added to tooth rows at least throughout the juvenile period. Absolute size, or ratios of absolute sizes (Olson, 1951: 108) were found to be meaningless, being related apparently either to food supply or to unknown physiologic or genetic factors. Size of recent fish, too, or of their component parts, varies immensely within the same age group in a particular pond, as veteran fishermen know. The angles between tooth rows remain constant with age in all but an occasional individual.

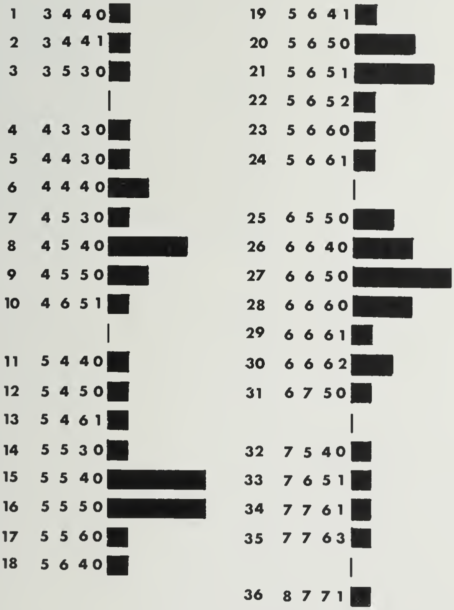


Fig. 5. Four feet above the base of the Greene Formation, pterygoid cusp number frequency histogram. The numbers on the left are step numbers. The following numbers are the numbers of cusps in rows A, B, C, and D, respectively.

PALATE AND CUSP NUMBERS, M. DUNKARDENSIS

Palates from the base of the Greene Formation differ most noticeably from those of older horizons in the numbers of individuals lacking cusps or having only one cusp in row D, almost 85% of the sampled individuals (Table 3). By contrast, only 54% of the palates from the base of the Upper Washington contain one or no cusps in row D (Table 6). That these figures do not reflect a significant difference in age composition of the two populations will become clear from a study of the remainder of the data.

When individual rows of cusps are counted, palates from the Greene have the greatest frequency of occurrence in row A at 5, with 42% of the sample. Row B has 6, at 44%; row C has 5, at 38%, and row D has 0, at 65%. The greatest combined frequency of occurrence in rows A and B is 5 and 6, and 6 and 6, each at 20.3%. In C it is 6 and 5, at 23%, and in C and D it is 5 and 0, at 27% (Tables 1, 2, 3). If one assembles an ideal individual from these figures that best represents the sample,

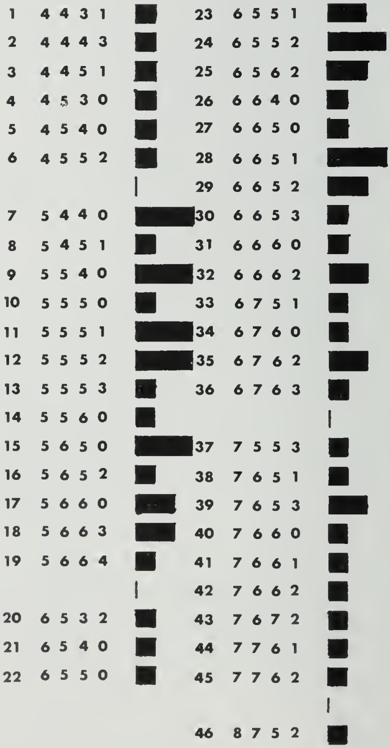


Fig. 6. Base of the Upper Washington Limestone, pterygoid cusp number frequency histogram. See fig. 5 for explanation.

it will have an A, B, C, D formula of 5, 6, 5, 0 or 6, 6, 5, 0. The ranges are 3-8, 3-9, 3-9, 0-4.

By contrast, palates from the base of the Upper Washington Limestone show that the greatest frequency of occurrence of cusps in row A is 6, at 38%; in row B, 6 at 39%; in row C, 5 at 50%; and in row D, 0 at 32%. The greatest combined frequency of occurrence in rows A and B is 5 and 5, at 17%; in B and C 5 and 5 at 23%; and in C and D, 5 and 1, at 18% (Tables 4, 5, 6). The most typical individual would thus have an A, B, C, D tooth-formula of 5, 5, 5, 1. The ranges are 4-8, 4-7, 3-7, 0-4.

M. DUNKARDENSIS, PTERYGOID ELEMENTS, HORIZON 4 FEET ABOVE BASE OF GREENE FORMATION

Table 1. 69 individuals.

	No. of				Row B				Total
	Cusps	2	3	4	5	6	7	8	
	3		1.44	1.44					2.89
	4		1.44	5.79	10.14	1.44			18.84
Row	5			4.34	17.39	20.28			42.02
A	6			2.89	20.28		2.89		26.08
	7				1.44	2.89	2.89	1.44	8.69
	8						1.44		1.44
			2.89	11.59	33.33	44.92	7.24	1.44	99.96

Table 2. 75 individuals.

	No. of			Row C				Total
	Cusps	3	4	5	6	7	8	
	3	1.33						1.33
	4	1.33	4.00	1.33	1.33			8.00
Row	5	5.33	15.60	15.60	1.33			36.00
B	6		7.09	22.69	17.33			45.33
	7			1.33	4.00	2.83		8.00
	8							
	9						1.33	1.33
		8.00	25.33	38.66	24.00	2.83	1.33	99.99

Table 3. 79 individuals.

	No. of			Row D			Total
	Cusps	0	1	2	3	4	
	3	7.59					7.59
	4	22.78	1.26				24.04
Row	5	27.84	10.12	1.26			39.24
C	6	6.32	7.59	6.32	1.26	1.26	22.78
	7		1.26	2.53			3.79
	8			2.53			2.53
		64.63	20.23	10.64	1.26	1.26	99.97

Values in tables above expressed in percent of total individuals

The trends of maximum cusp frequency indicate that in the Greene Formation sample, cusps are added to rows A, B, and C so that rows A and B are usually equal and C is usually one cusp behind. After the 5th cusp in C, a cusp is usually added to start row D, and then cusps are added equally in all rows. The same picture is generally true for the Upper Washington sample, but row C more often is equal to the first two rows, and row D is usually started at C = 4.

M. DUNKARDENSIS, PTERYGOID ELEMENTS,
BASE OF UPPER WASHINGTON LIMESTONE

Table 4. 68 individuals

	No. of Cusps	Row B 4	5	6	7	Total
	4	4.41	4.41			8.82
Row	5	5.88	17.64	13.23		36.75
A	6		14.70	16.17	7.35	38.22
	7		1.47	10.29	2.94	14.70
	8				1.47	1.47
		10.29	38.22	39.69	11.76	99.96

Table 5. 68 individuals

	No. of Cusps	Row C 3	4	5	6	7	Total
	4	1.47	5.88	2.94			10.29
Row	5	2.94	7.35	23.52	4.41		38.23
B	6		1.47	20.58	16.17	1.47	39.70
	7			2.94	8.82		11.76
		4.41	14.70	50.00	29.41	1.47	99.98

Table 6. 68 individuals

	No. of Cusps	Row D 0	1	2	3	4	Total
	3	1.47	1.47	1.47			4.41
Row	4	13.23			1.47		14.70
C	5	8.82	17.64	16.17	7.35		50.00
	6	8.82	2.94	11.76	4.41	1.47	29.41
	7			1.47			1.47
		32.35	22.05	30.88	13.23	1.47	99.99

Values in tables above expressed in percent of total individuals

Frequency histograms of specimens in which all 4 rows can be reliably counted provide some insight into variation through growth stages. For the Greene sample (fig. 5), peaks occur at steps 6, 8, 9, 15, 16, 20, 21, 25, 26, 27, 28, and 30. Within this scheme, addition of cusps may proceed from step 6 to 8 to 9 to 16 to 20 to 21 or to 27 to 28 to 30.

Obvious alternate pathways exist, such as 6 to 8 to 15 to 26, or 15 to 16 to 25 to 27. Peak occurrences thus may represent not only preferred pathways but preferred intersections of different pathways, like steps 16 and 27. This scheme will be developed in the discussion of the lower jaws.

The frequency histogram for the palates of the Upper Washington sample (fig. 6) shows considerably greater representation of individuals with 6 or 7 cusps in row A than does the Greene histogram. The sample thus seems to include a larger number of somewhat older individuals. This unfortunately may be a result of breakage of one or more rows in many of the Greene specimens, for only 63 individuals out of 112 could be used for this evaluation. Nevertheless, it is clear from figure 6 that there is no one way to produce a later-step jaw from an earlier-step jaw, and that the peaks represent preferred combinations through the A = 7, the oldest individuals being well represented in row D = 0, as at every level of A.

All cusp-number variation indicates the similarity of development in rows A, B, and C between the Upper Washington base and the base of the Greene. The patterns of row D contrast quite strongly between the two samples at the same levels of development of row A, where A = 4, 5, or 6.

PREARTICULAR AND CUSP NUMBERS, M. DUNKARDENSIS

Prearticular dentitions from the base of the Greene Formation differ from those of older horizons most noticeably in the numbers of individuals lacking cusps or having only one cusp in row C, 21% of the individuals in the sample. This is morphologically consistent with the lack of row D in some of the pterygoids, but numerically very disproportionate. It contrasts strongly with the Upper Washington sample, where no individuals have fewer than 2 cusps in row C, and may represent a developmental "anomaly" similar to that of the single-bladed prearticulars of *M. stenodonta* (Lund, 1970b).

Cusp counts of individual prearticular rows from the base of the Greene (Tables 7, 8) show that the greatest frequency of occurrence in row A is 5, at 39%; in row B, 5, at 46%, and in row C, 3, at 29%. The greatest combined frequency of occurrence in rows A and B is 5, 5, and 6, 5, each at 18%; in B and C 5, 4, also at 18%. An ideal individual that best fits the sample would have an A, B, C formula of either 5, 5, 4 or 6, 5, 4. The ranges are 4-7, 3-6, 0-6.

Prearticulars from the base of the Upper Washington (Tables 9, 10) show that the greatest frequency of occurrence of cusps in row A is 6, at 42%; in row B, 4, at 48%; and row C, 3, at 42%. The greatest combined frequency of occurrence in rows A and B is 6, 5, at 28%. B, C is 4, 3, at 23%. A best-fit individual would have a formula of 6, 5, 3, or

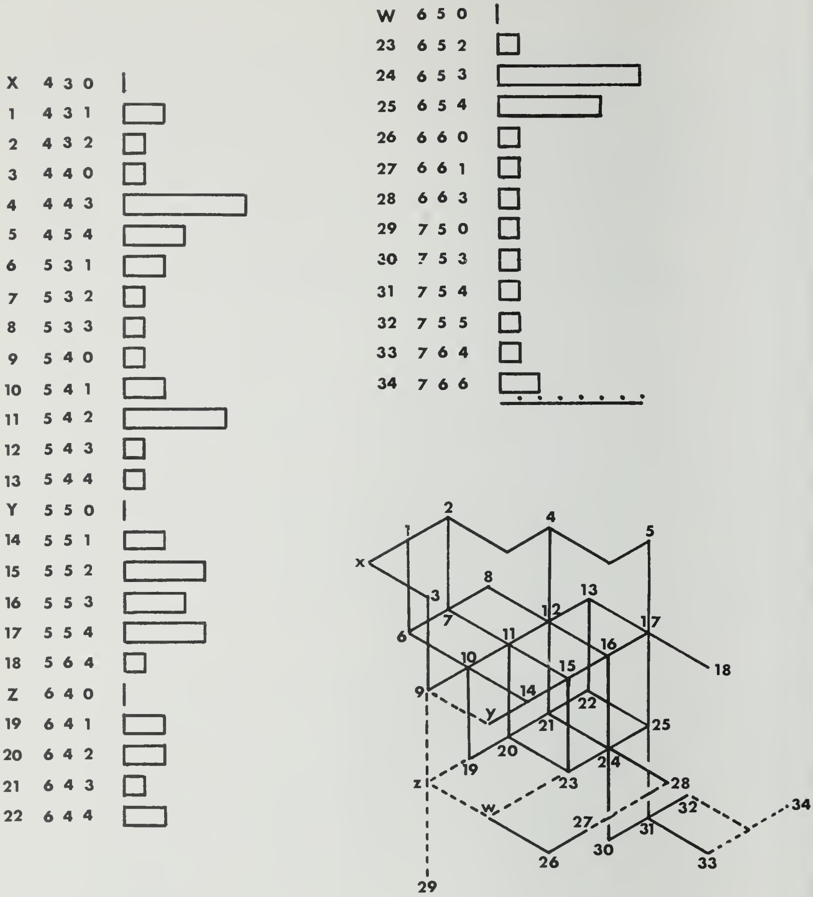


Fig. 7. Four feet above the base of the Greene Formation, prearticular cusp number frequency histogram and cusp addition chart. The numbers on the chart are step numbers. Letters represent steps not present in the sample. A vertical line segment represents the addition of a cusp in row A; a line segment from upper left to lower right, the addition of a cusp in row B; and a line segment from lower left to upper right the addition of a cusp in row C.

perhaps 6, 5, 4. The ranges are 3-9, 3-6, 2-5.

The trends of maximum cusp frequency indicate that in the Greene Formation sample, cusps are added to rows A, B, and C so that rows A and B are usually equal, and that C usually has one less cusp. In the Upper Washington sample, however, an inequality of cusp numbers in rows A, B, and C is typical: A generally has one more cusp than B, and B usually has one more (one or two more in B = 5) than row C.

PREARTICULAR ELEMENTS, *M. DUNKARDENSIS*, HORIZON 4 FEET ABOVE BASE OF GREENE FORMATION

Table 7. 71 individuals

	No. of	Row B				Total
	Cusps	3	4	5	6	
	4	4.225	9.859	4.225		18.309
Row	5	5.633	14.084	18.309	1.408	39.434
A	6		9.859	18.309	4.225	32.393
	7			5.633	4.225	9.858
		9.858	33.802	46.476	9.858	99.994

Table 8. 71 individuals

	No. of	Row C							Total
	Cusps	0	1	2	3	4	5	6	
	3		5.633	2.816	1.408				9.857
Row	4	2.816	5.633	9.859	11.267	4.225			33.800
B	5	1.408	2.816	7.042	15.492	18.309	1.408		46 475
	6	1.408	1.408		1.408	2.816		2.816	9.856
		5.632	15.490	19.717	29.577	25.350	1.408	2.816	99.988

Values in tables above expressed in percent of total individuals

M. DUNKARDENSIS, PREARTICULAR ELEMENTS, BASE OF UPPER WASHINGTON LIMESTONE

Table 9. 69 individuals

	No. of	Row B				Total
	Cusps	3	4	5	6	
	3	1.449				1.449
	4	1.449	15.942			17.391
Row	5	1.449	20.289	11.599		33.337
A	6		10.144	28.985	2.898	42.027
	7		1.449	1.449	1.449	4.347
	8					
	9			1.449		1.449
		4.347	47.824	43.482	4.347	100.000

Table 10. 69 individuals

	No. of	Row C				Total
	Cusps	2	3	4	5	
	3	2.898	1.449			4.347
Row	4	7.246	23.188	17.391		47.825
B	5		17.391	17.391	7.246	42.028
	6			2.898	1.449	4.347
		10.144	42.028	37.680	8.695	98.547

Values in tables above expressed in percent of total individuals

To develop a visible model of cusp addition, frequency histograms have been coupled with isometric diagrams illustrating the possible pathways between specimens (figs. 7, 8, 9). In these figures, each line segment represents the addition of one cusp in row A, B, or C. Thus step 6 (fig. 7), formula 5, 3, 1, is represented by 2 specimens. Step 7, formula 5, 3, 2, represented by one specimen, may be derived from step 6 by the addition of a cusp in row A. Steps that are not represented by specimens, yet seem to have been necessary, are indicated by letters. These hypothesized pathways are indicated by broken lines. Pathways not specifically dictated by specimens have been omitted.

It has been demonstrated in the preceding discussion that for every cusp addition in row A there are corresponding additions in the succeeding rows, which follow a basic pattern peculiar to that jaw at that horizon. For convenience, I shall refer to each level of row A as a

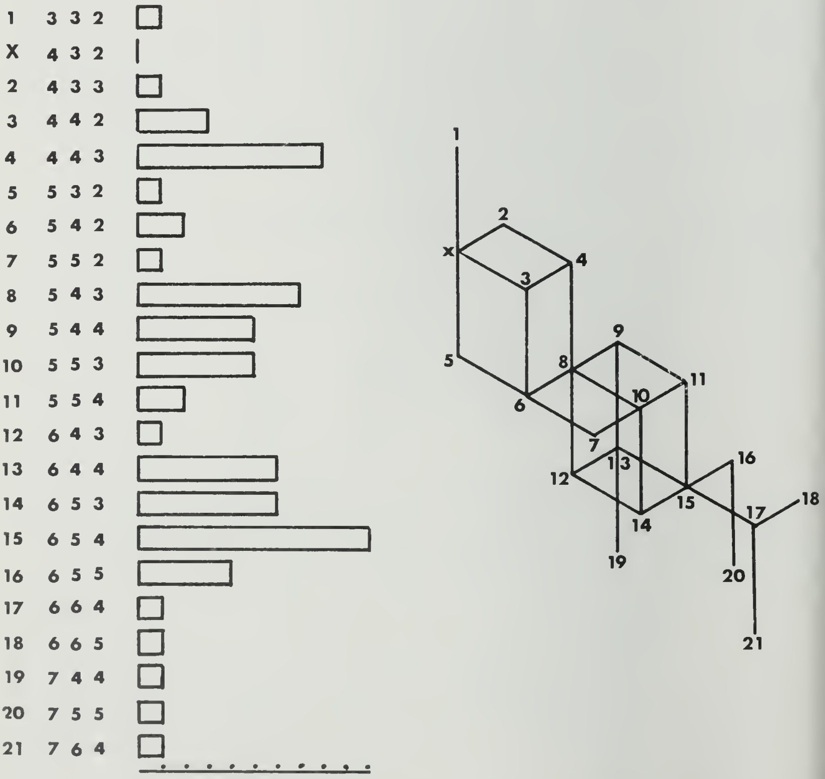


Fig. 8. Base of the Upper Washington Limestone, prearticular cusp number frequency histogram and cusp addition chart. See fig. 7 for explanation.

growth stage, and to each addition of cusps in the other rows as steps within that stage.

The variety of different tooth-row counts on the prearticulars of the Greene sample is wide, although the number of stages is only 4 (fig. 7). The frequency histogram contains one major peak of 5 or more specimens for stages A = 4 (stage 4) and A = 5 (stage 5), and 2 adjoining peaks for stage 6. There are too few specimens of stage 7 to expect any significant frequency distribution. The major peaks occur at steps 4, 11, 24, and 25. Secondary peaks of 3 or 4 specimens occur at different steps within each stage, at 5, 15, 16, and 17. The pattern of prearticular tooth addition in this sample would seem to show a preferred pathway through steps 4, 5, 17, and 25 to the A = 7 stage. The ideal individual of the previous discussion would correspond to step 17 or step 25.

The tooth addition model for prearticulars from the Upper Washington sample (fig. 8) has a much simpler pattern. There are more specimens concentrated at the major peaks in each of the A = 4, 5, and 6 stages, and the minor peaks of each stage are clearly related to the major peaks. In essence, all individuals but one (step 7) pass through step 8 in the A = 5 stage, and all individuals but one (step 19) pass through step 15 in the A = 6 stage. The pattern of tooth addition in the Upper Washington prearticulars is strictly controlled, so that there is almost unvarying close relationship between the three rows at any one time; i.e., a very narrow developmental pathway yields the various growth stages found in the sample.

While there is evidently some relationship between rows in the Greene sample the relationship is a rather loose one, the broad variation in development resulting in part from the persistent reservoir of D = 0 and underlining a breakdown of row relationships. A review of figure 5 indicates that the same stability of pattern seen in the prearticulates of the Upper Washington sample characterizes the essentially three-ridged pterygoids of the Greene sample. Figure 6, of the Upper Washington sample, shows an increased degree of variability consistent with the presence of row D, but is also a fairly stable, conservative pattern. Variation of pathways centers around the development of cusps in row D. No significant breakdown of row relationships corresponding to the Greene prearticulars is seen in the Greene pterygoids, which are consistent with the pattern seen in the Upper Washington.

CUSP NUMBERS, MONONGAHELA STENODONTA

To date, only the Duquesne Limestone has yielded enough individuals for analysis, although work continues on a locality in the Lower Washington Limestone. Cusp counts of individual pterygoid rows from Du-

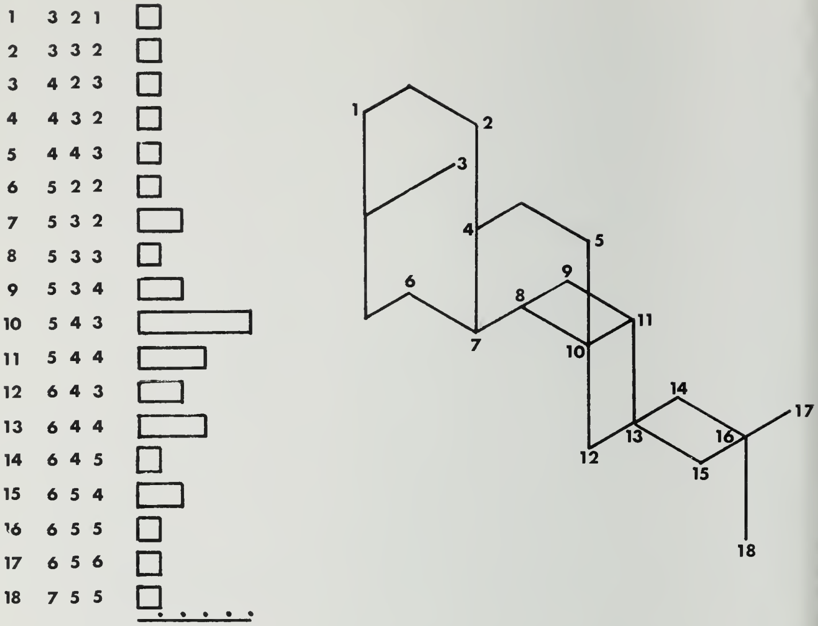


Fig. 9. Duquesne Limestone 2A, *Monongahela stenodonta,* prearticular cusp number histogram and cusp addition chart. See fig. 7 for explanation.

quesne Limestone 2A show that the maximum frequency of cusp occurrence in row A is 5, at 35%; in row B, 6, at 48%; in row C, 4, at 54%; and in row D, 3, at 41%. The greatest combined frequencies of occurrence are: A and B, 5 and 5, 6 and 6, and 7 and 6, each at 17.4%; B and C, 5 and 4 at 32%, and C and D at 4 and 3, at 41%. A statistical "best fit" individual would have a formula 5, 5, 4, 3. The ranges are 4-7, 3-6, 3-6, 0-5 (Tables 11-13), which indicate that A adds 3 cusps (cusps 5-7) to one of row B (cusp 6), whereas C adds no cusps past 4 until D = 3. At this (usually the A = 6) stage, indications are that cusp addition proceeds relatively uniformly from A through D. B is thus the longest row in the earlier stage individuals of our sample, addition of cusps then taking place at A and D until a relatively uniform set of 4 rows is established.

Maximum frequency of occurrence of cusp numbers in the prearticular dentition (Tables 14, 15) is A = 5, at 46.6%, B = 4, at 50%, and C = 3 or 4, each at 33.3%. The maximum combined frequencies are: A and B, 5 and 4, at 26.6%; and B and C, 4 and 3 at 26.6%. The statistical "best fit" would have a formula of 5, 4, 3. The ranges are 3-7, 2-5, 1-6. The statistical best fit individual does actually fit, as shown by fig. 9.

Although the sample contains so few individuals that only the A = 5 and A = 6 stages are adequately represented, the maximum frequency pathway clearly lies through steps 7, 8, 10, 11, 13, and 15 or 7, 8, 9, 11, 13, and 15. The latitude of developmental variation is exceedingly limited.

ANGULAR VARIATION, MONONGAHELA DUNKARDENSIS

Measurements of angles between tooth rows of angles AB and BC of the pterygoids are defined by rows A, B, and C. Pterygoids from the Greene sample (fig. 11) yield the following statistical data: Mean AB is 14.37°, extremes are 7° and 28°; standard deviation is 3.37. The mean BC is 15.49°, extremes are 9° and 32°, standard deviation is 3.71°. The Pearson correlation coefficient between angles is .6432, and the slope of the regression line is .7089. Only 2 of the 99 specimens measured fall outside 3 S.D.

PTERYGOID ELEMENTS, *M. STENODONTA*, DUQUESNE LIMESTONE 2A

Table 11. 23 individuals

	No. of Cusps	Row B				Total
		3	4	5	6	
Row A	4			13.04	4.34	17.38
	5	4.34	4.34	17.39	8.69	34.76
	6			13.04	17.39	30.43
	7				17.39	17.39
		4.34	4.34	43.47	47.81	99.98

Table 12. 22 individuals

	No. of Cusps	Row C				Total
		3	4	5	6	
Row B	3		4.54			4.54
	4		4.54			4.54
	5		31.81	9.09		40.90
	6		13.63	13.63	22.72	50.00
			54.54	22.72	22.72	99.98

Table 13. 22 individuals

	No. of Cusps	Row D						Total
		0	1	2	3	4	5	
Row C	4	9.09	9.09	13.63	22.72			54.54
	5			4.54	13.63	4.54		22.72
	6				4.54	13.63	4.54	22.72
		9.09	9.09	18.18	40.90	18.18	4.54	99.98

Values in tables above expressed in percent of total individuals

PREARTICULAR ELEMENTS, *M. STENODONTA*, DUQUESNE LIMESTONE 2A

Table 14. 30 individuals

				Row B			Total
	No. of Cusps	2	3	4	5	6	
	3	3.333	3.333				6.666
Row A	4	3.333	3.333	3.333			9.999
	5	3.333	16.666	26.666			46.665
	6			20.000	13.333		33.333
	7				3.333		3.333
		9.999	23.332	49.999	16.666		99.996

Table 15. 30 individuals

				Row C				Total
	No. of Cusps	1	2	3	4	5	6	
	2	3.333	3.333	3.333				9.999
Row B	3		13.333	3.333	6.666			23.332
	4			26.666	20.000	3.333		49.999
	5				6.666	6.666	3.333	16.665
		3.333	16.666	33.332	33.332	9.999	3.333	99.995

Values in tables above expressed in percent of total individuals

The two measured angles are closely correlated, and the angles form a tight group graphically (fig. 11). Generally speaking, the larger the angle BC, the larger the angle AB.

The pterygoids from the Upper Washington sample (fig. 10) yielded the following information: Mean AB is 17.50°, with extremes of 10° and 30°; standard deviation is 4.06; mean BC is 20.79°, with extremes of 13° and 35°; the standard deviation is 4.20. The Pearson Correlation coefficient is .5272, and the slope of the regression line is .5445. One of 87 specimens falls outside of 3 standard deviations. The Greene sample has a somewhat smaller mean then the Upper Washington, a slightly tighter grouping with greater scattering within the group, and a slightly steeper slope on the regression line. Each sample forms a homogenous group with little deviation from it.

The prearticulars from the Greene sample (fig. 13) yielded the following information: Mean AB is 23.3°, with extremes of 14° and 35°, and standard deviation 4.56; mean BC is 26.96°, with extremes of 14° and 75°, and standard deviation 10.9128; the correlation coefficient is .0664. One of the 76 specimens lies considerably above 3 SD.

The Upper Washington sample (fig. 12) yielded the following information: Mean AB is 25.63°, with extremes of 14° and 39°, and standard deviation 5.4548; mean BC is 38.32°, with extremes of 18° and 76°, and standard deviation 11.8549; the correlation coefficient is .0424. One of the 88 specimens lies above 3 SD.

Neither of the samples shows any real correlation between angles AB and BC (figs. 12, 13). The mean of angle AB is slightly smaller in the Greene sample, the grouping is tighter at lower values of BC, with fewer specimens outside the group and more duplicate readings in the group. The distribution of specimens along the BC axis in the Upper Washington sample shows a slight concentration toward lower BC values. The Greene sample falls into a tight group below BC = 30° and a loose collection of individuals tapering off to one individual at 75°.

Mean angle AB of the prearticulars of the Greene sample is 9° larger than the corresponding angle of the pterygoid. The mean angle AB of the Upper Washington prearticulars is 8.1° larger than that of the pterygoids, and the mean angle BC is 17.5° larger. The differences between tooth-row angles in the upper and lower jaws is surprisingly small in view of the wide variation in prearticular angles.

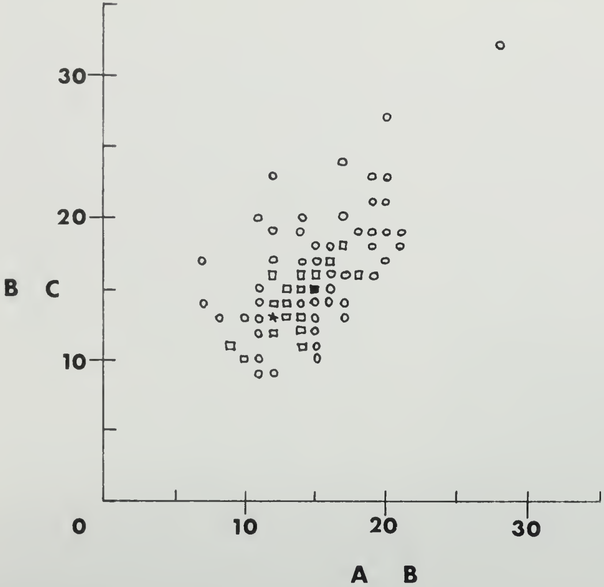
ANGULAR VARIATION, MONONGAHELA STENODONTA

The pterygoids of the Duquesne Limestone sample (fig. 14) yielded the following statistics: Mean AB is 41.65°, with a range of 22° to 60°, and standard deviation 5.9692; the correlation coefficient is .09 and the slope of the regression line .0766. One important factor must be emphasized, that the two angles approximate or equal 90° in all but 2 specimens (fig. 14). Statistical data for the prearticulars are: Mean AB is 43.80°, with a range of 25° to 71° and a standard deviation of 10.24; mean BC is 69.55° with a range of 40° to 110° and a standard deviation of 15.53; the correlation coefficient is .0695 and the slope of the regression line is —.9249. In figure 15, BC apparently separates into 2 groups at AB greater than 45°, which may reflect a relationship with angle CD of the pterygoid. This has not yet been tested.

QUALITATIVE VARIATION

Many variables can be observed among individuals of either population of *M. dunkardensis*. Two classes of variables have been measured, but others must be considered as well. In the pterygoids from the Greene population, a noticeable tendency exists to form a heel through growth and wear. The heel may seem to be an inevitable result of growth and wear in closely aligned tooth rows, but it does not show up in all specimens of equivalent stages, and is much less prevalent among members of the Upper Washington population. It is not seen in *M. stenodonta*, where the tooth rows differ basically in shape and occlusal relationships.

The shapes of the central cores of individual cusps tend to be transverse to the axis of the rows in all rows in most specimens from the Greene. There are a fair number of specimens from the Upper Wash-



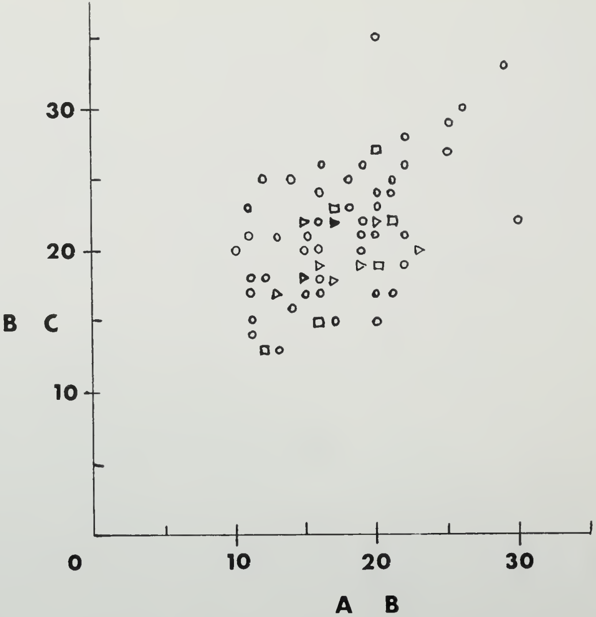
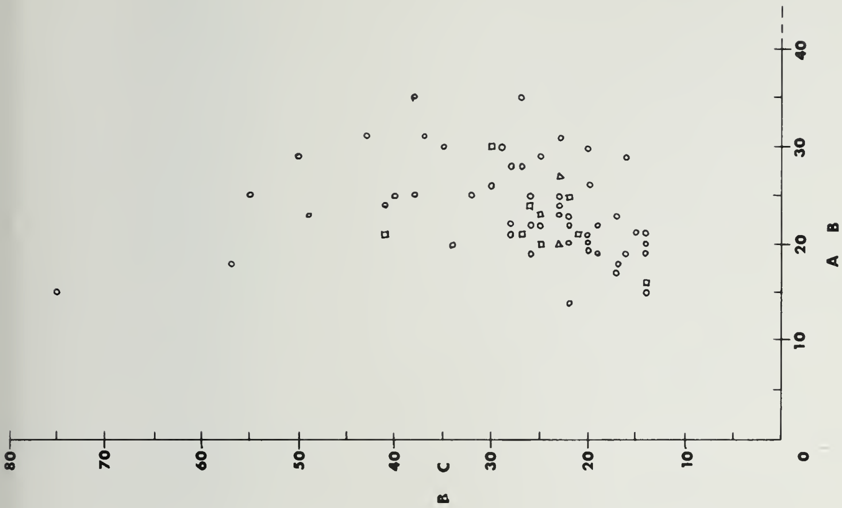


Fig. 10 (above L.). Base of the Upper Washington Limestone, pterygoids, relationship between angles AB and BC. Fig. 11 (above R.). Four feet above the base of the Greene Formation, pterygoids, relationship between angles AB and BC. Symbols indicate number of individual jaws. (See figs. 12 & 13 for explanation.)

Fig. 12 (below L.). Base of the Upper Washington Limestone. prearticulars, relationship between angles AB and BC. Fig. 13 (below R.). Four feet above the base of the Greene Formation, prearticulars, relationship between angles AB and BC.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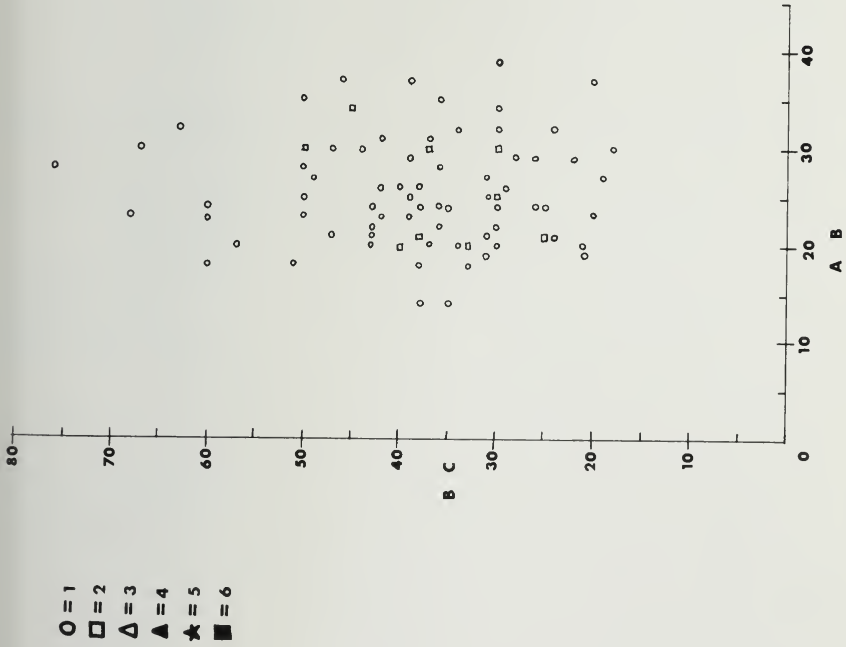
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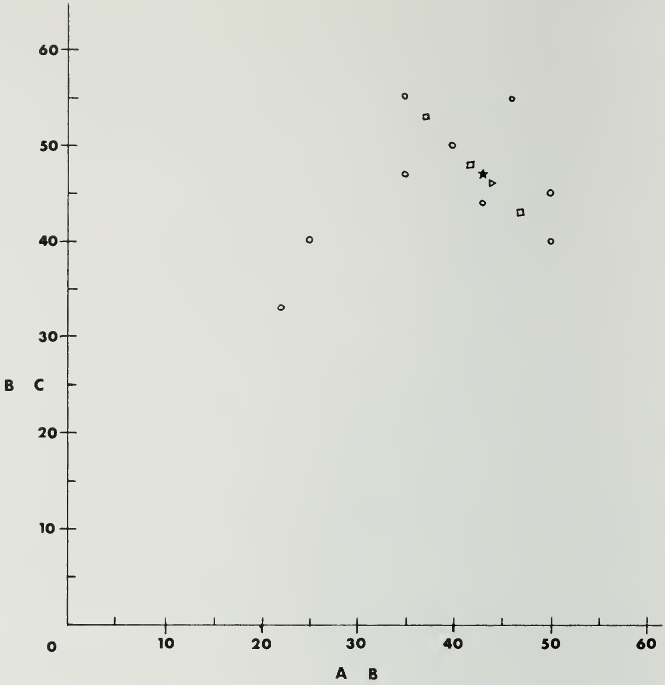

Fig. 14. Duquesne Limestone, *Monongahela stenodonta,* pterygoids, relationship between angles AB and BC. (See figs. 11, 12, & 13 for explanation of symbols.)

ington which have round cores in row A. In the narrow, bladelike tooth rows of *M. stenodonta* the cores are basically conical prisms.

The thickness of the bone at and near the symphysis of both pterygoid and prearticular is considerably greater in the later stages of Greene individuals than in the same stages of Upper Washington individuals. The thickness of the tooth plate itself increases dramatically with size and with stage in most Greene specimens.

Significant departures from the basic pattern of this species occur in only a few prearticulars where no teeth are present on a spur of bone and dentine, representing row C (fig. 4). The spur remains so low as to have evidently never emerged from the gum. This clearly represents some sort of failure of the mechanism that would induce individual tooth formation, possibly an absence of ameloblast organizer for that row. These specimens are confined to the Greene sample.

By contrast, in *Monongahela stenodonta* fine variation, apart from height of the tooth blade or thickness of the tooth row, which are strictly related to growth stage, is not particularly noticeable. Gross varia-

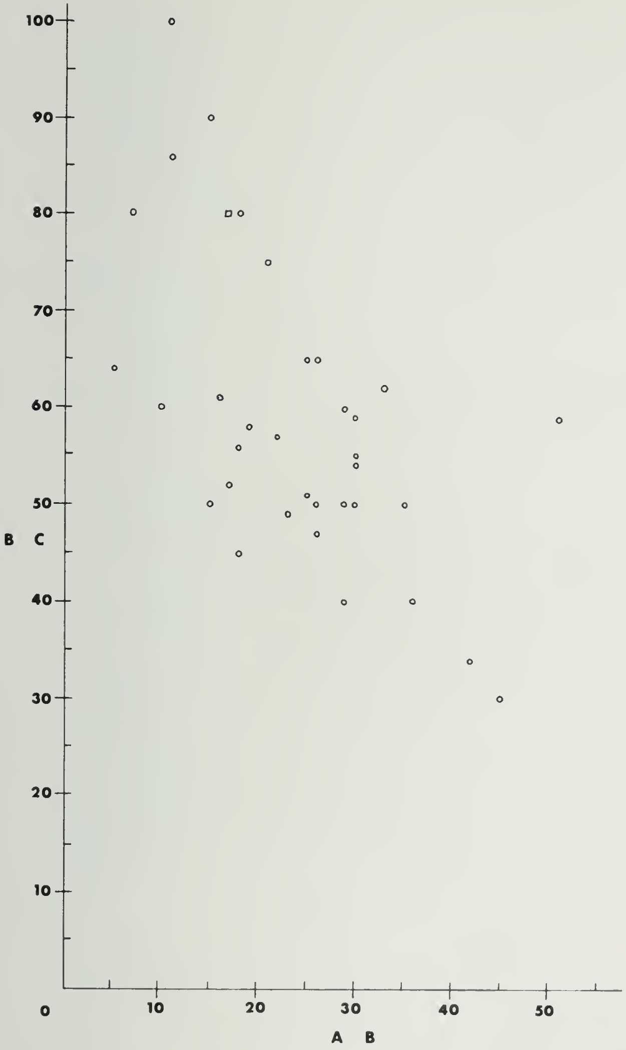

Fig. 15. Duquesne Limestone, *Monongahela stenodonta,* prearticulars, relationship between angles AB and BC. (See figs. 11, 12, & 13 for explanation of symbols.)

tions from the "normal" basic pattern are so common as to render the term "normal" all but meaningless in the Lower Washington Limestone. Such variations are only slightly less common in the Duquesne Limestone. Single-bladed prearticulars have been discussed elsewhere, (Lund, 1970b: 255-257) and seem to characterize *M. stenodonta* wher-

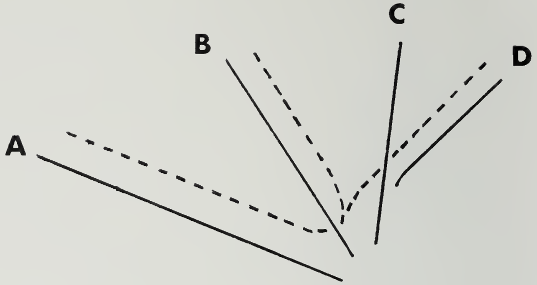

Fig. 16. Occlusal patterns in *Monongahela.* Solid lines represent pterygoid tooth rows, dashed lines represent prearticular tooth rows. Rows A, B, C, and D (pterygoid only) labeled from anterior to posterior.

ever it is found. Subsequent to the above publication, corresponding anomalies in the pterygoids have been found. These anomalies occur in several ways. A single-bladed pterygoid, from the Lower Washington (Specimen field number 35) shows the same type of dwarf cusps at its posterior end as in the prearticulars, representing rows B and C, with one cusp each. Specimens occur with an elongate row A, 2 or 3 cusps in row B, and either one cusp in row C or simply a ridge of bone and dentine (fig. 3). Row A may or may not be worn abnormally. Row B is unworn, indicating that it had not erupted or did not properly occlude. Two specimens are known with supernumerary rows, one a prearticular in which an extra row is found between rows B and C, the other a pterygoid in which an extra row is intercalated between rows C and D (fig. 3). One pterygoid from the Duquesne Limestone and one from the Lower Washington Limestone show the development of multiple cores in the tooth ridges with increased size, a feature that obscures cusp identification as wear progresses, leaving a uniform blunt ridge. Both specimens also show additional differences in tooth-row origin and orientation that presage *Gnathorhiza dikeloda* from the Permian of Texas (Olson, 1951). It is not certain whether the presence of subsidiary cusps on occasional other specimens reflects the presence of subsidiary cores as well.

Monongahela stenodonta carries a large load of anomalies, qualitative developmental deviations of one sort or another. Only one of these anomalies is found in *M. dunkardensis,* the omission of discrete teeth on a row. Further, while this feature is accompanied by other defects in the pterygoids of *M. stenodonta,* it has been found only on otherwise normal prearticulars in the Dunkard species.

DISCUSSION

Jaws with angular relationships recognizably different from normal *Monongahela stenodonta* occur in small numbers in the Duquesne Limestones. These jaws have angles between tooth plates on the pterygoids that are significantly smaller than the normal jaws. (fig. 14). They also do not follow the pattern of complementary angles approximating 90° that typifies this species at this time. Jaws with small angles are also found in the Lower Pittsburgh Limestone together with normal *M. stenodonta.*

The Washington Formation contains lungfish remains in which there are, for the first time, clearly recognizable separate populations of *M. stenodonta* and *M. dunkardensis,* a narrow-angled form. In rocks younger than this horizon only *M. dunkardensis* has been found.

Many changes occur between the first known occurrences of narrow angles in the Conemaugh and the latest population from the base of the Greene Formation. The narrow jaws from the Conemaugh have considerably wider angles and have narrower blades than any younger specimen. The Dunkard populations show a progressive delay in the start of pterygoid row D, a progressive change to a crushing heel rather than shearing ridges on the pterygoid, along with thickening of the jaw bones and tooth ridges, and a decrease in the latitude of variation of the prearticular dentition. There is also a slight decrease in the mean of each angle of the pterygoids. The pattern of tooth-row growth remains essentially the same in earlier *M. dunkardensis* as in *M. stenodonta* until the Greene, where it diversifies greatly.

The pattern of species differentiation is divisible into three phases. The first phase starts with one small portion of the parent stock, *M. stenodonta,* containing an anomalously narrow set of angles between tooth ridges, but not incorporating any of the other striking anomalies of the parent stock. This variety, apparently existing completely sympatrically with its parent, becomes more common and the angles become tighter and more uniform, particularly on the pterygoid, throughout the Conemaugh and Monongahela. A slight degree of habitat differentiation becomes evident to mark phase two, around the time of the Lower Washington Limestone, for the two types are found in slightly differing portions of the same silty limestone bed. Morphological differentiation, as expressed in the shapes of the tooth ridges and their cores, progresses to the extent that portions of the tooth rows of individuals of the two kinds are readily distinguishable. At this point, they could be called separate species. Phase three involves further morphological change, in the angles, the cores, development of the heel, thickening of bone and tooth, and developmental changes like the pattern of tooth-row growth and the tendency to lose row D of the pterygoid or row C of the prearticular. These last changes are innovative, peculiar to the new species, setting it further apart from the parent stock. The parent stock continues into the Lower Washington, with its load of anomalies, but with very little change. It has not yet been found above the Lower Washington in this area, but certainly migrates westward to give rise to members of the genus *Gnathorhiza.*

Little of note can be found in the geologic record relevant to these changes. The Washington Coal contains evidence that the great Pennsylvanian epicontinental sea transgressed as far east as Belmont County, Ohio, at this time (Berryhill, 1963). After this, with the final retreat of the sea and increased uplift and sediment influx connected with the Appalachian orogeny, it is conceivable that the coastal plain environment favored by *M. stenodonta* retreated to the west and southwest. The changing environment on the upper delta plain of the rising Appalachian Mountains, however, provided a good setting for further differentiation of *M. dunkardensis.*

The dietary preferences of *M. dunkardensis* are difficult to assess. The crushing or grinding dentition may have been most useful upon small arthropods like ostracods, which were very common at that time. The Greene population was extracted from an ostracodal sand lens. It is also possible that this dentition may have been used upon plant debris or organism-filled muds, a possibility reinforced by the occurrence of this lungfish, in beds below the Greene population, chiefly in rocks containing a very high percentage of macerated plant debris.

REFERENCES CITED

ARKLE, T., JR.

1959. Monongahela Series, Pennsylvania System, and Washington and Greene Series, Permian System, of the Appalachian Basin. *In* Geol. Soc. Amer. Guidebook, Pittsburgh Meeting, 115-141.

BAIRD, D.

1962. A haplolepid fish fauna in the early Pennsylvania of Nova Scotia. Paleontology, 5(1). 22-29.

BERMAN, D. S.

1968. Lungfish from the Leuders Formation (Lower Permian, Texas) and the *Gnathorhiza*-lepidosirenid ancestry questioned. Jour. Pal., 42(3):827-835.

BERRYHILL, H. L., JR.

1963. Geology and coal resources of Belmont County, Ohio. U. S. Geol. Surv. Prof. Paper 380: 113 pp.

CARLSON, K. J.

1968. The skull morphology and estivation burrows of the Permian lungfish *Gnathorhiza serrata.* Jour. Geol., 76: 641-663.

CLENDENING, J. A.

1969. The base of the Permian in the Appalachians, ninety years of controversy. *In,* Some Appalachian Coals and Carbonates: Models of Ancient Shallow-Water Deposition: 229-233. W. Va. Geol. Surv., Morgantown.

DARRAH, W. C.
1935. American Carboniferous floras. Second Heelen (Holland) Carboniferous Congress, Summary of Paper. Issued from the Botanical Mus., Harvard Univ.
LUND, R.
1970a. A new technique for chemical preparation of fossils. Jour. Pal., 44(3): 578.
1970b. Fossil fishes from southwestern Pennsylvania, Part I: Fishes from the Duquesne Limestones (Conemaugh, Pennsylvanian). Ann. Carnegie Mus., 41(8): 231-261.
MORAN, W. E.
1952. Location and stratigraphy of known occurrences of fossil tetrapods in the Upper Pennsylvanian and Permian of Pennsylvania, West Virginia and Ohio. Ann. Carnegie Mus., 33(1): 1-44.
MORRIS, D. A.
1968. Lower Conemaugh (Pennsylvanian) depositional environments and paleogeography in the Appalachian coal basin. Univ. Microfilms, Ann Arbor. 521 pp.
NEWBERRY, J. S.
1875. Descriptions of fossil fishes. Geol. Surv. Ohio, 2(2): 1-64.
OLSON, E. C.
1951. Fauna of the Upper Vale and Choza. 3. Lungfish of the Vale. 4. The skull of *Gnathorhiza dikeloda* Olson. Fieldiana Geol., 10: 104-124.
PEPPERS, R. A.
1964. Spores in strata of late Pennsylvanian cyclothems in the Illinois Basin. Ill. Geol. Surv. Bull., 90: 9-89.
RAYMOND, P. E.
1910. A preliminary list of the fauna of the Allegheny and Conemaugh Series of western Pennsylvania. Ann. Carnegie Mus., 7: 144-158.
ROMER, A. S.
1952. Late Pennsylvanian and early Permian vertebrates of the Pittsburgh-West Virginia region. Ann. Carnegie Mus., 33(2): 47-112.
1958. The Texas Permian redbeds and their vertebrate fauna. *In* Studies on Fossil Vertebrates, ed. by T. S. Westoll: 157-179.
SMITH, C. L.
1956. A simple microscope protractor. Copeia, 4: 250.
STURGEON, M. T., AND R. D. HOARE
1968. Pennsylvanian brachiopods of Ohio. Ohio Geol. Surv. Bull., 63: 1-95.
WILLIAMS, D. G., J. C. FERM, A. L. GUBER, AND R. C. BERGENBACK
1964. Cyclic sedimentation in the Carboniferous of western Pennsylvania. *In,* Guidebook of 29th Ann. Field Conf. Penna. Geol., Penna. State Univ., University Park: 35 pp.

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ECOLOGICAL ASPECTS OF THE DISTRIBUTION OF SUBSOIL HERPETOFAUNA IN NDUMU GAME RESERVE

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Wayne F. Hadley[2]

Carl Gans[3]
Research Associate, Section of Amphibians and Reptiles

Introduction

The tropics are inhabited by numerous species of fossorial squamates, many of which show limb reduction. Most of the papers dealing with these refer to taxonomy or morphology, and relatively little is known regarding the factors influencing their distribution (Gans, 1968, 1971). The lack of such data is even more important in view of the rapid and sweeping ecological changes now occurring in many tropical areas. For this reason, the generation of preliminary ecological data was one of the aims of a survey trip (by Gans) to various African localities during 1969. (Gans completed work for his contribution to this paper while associated with the Department of Biology, State University of New York at Buffalo.)

The data presented here were obtained by A. C. Pooley in the Ndumu Game Reserve as a byproduct of an intensive program of collecting the amphisbaenian *Zygaspis violacea* (cf. Pooley, 1965, 1970 for miscellaneous records on the Ndumu herpetofauna). It is hoped that their availability will stimulate more intensive and extensive surveys of other areas.

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Submitted for publication Sept. 20, 1971.

NATURAL HISTORY SURVEY
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METHODS

All the surveys were carried out in Ndumu Game Reserve and adjacent area, in Zululand, South Africa, a locality that lies on an effective temperature line between 17° and 18° on Stuckenberg's (1969) map. The area receives approximately 700 mm of rainfall annually (Nuttonson, 1961), most of it falling from January through March (see South African Weather Bureau Publications 19, 22, 28, and 29 for more detailed climatological data). The seasonal climatic pattern of the area is influenced not only by rainfall changes, but also by the flooding of the Pongola River which fills the large pans adjacent to this area, usually during January to March. The study areas tend to be flooded intermittently at that time. This flooding pattern has now been interrupted by the construction of the J. G. Strydom Dam.

Ndumu, the only hill in the area, rises to 573 feet above sea level. Reports indicate that it is composed of red sands (Ibumdu) overlying Cretaceous strata at the base. The red sands contain much magnetite, and their grains are rounded and covered by some form of haematite, possibly indicating aeolian origin (K. L. Tinley, MS).

Four major habitats were sampled to a total of 524 square yards. All sample plots were dug to a standard depth of 2′6″, since previous collections have revealed no reptiles at greater depths. The collections reported here were assembled during March and April, 1970, except for the Group D excavation, which was made as a byproduct of construction work for crocodile pens.

DESCRIPTION OF AREAS

HABITAT GROUP A

The plots sampled were located on the Ndumu hill at elevations between 200 and 400 feet above sea level. A total of 496 square yards was sampled (fig. 1).

PLOT A.1: This plot included 360 square yards of firmly packed orange-red, fine sand. It included three vegetation types, each with an area of 120 square yards. These are referred to as subplots A.1.a, A.1.b, and A.1.c.

SUBPLOT A.1.a: This area was covered by sparse grasses, occasionally occurring in mats but with intermediate areas of exposed soil. Tufts of the grasses *Trichoneura grandiglumis, Pogonarthria squarrosa, Aristida congesta,* and *Aristida congesta barbicollis* were 9 to 30 inches tall. The soil was dry to a depth of 18 inches and contained clumps of tangled grass roots. Invertebrates were abundant at the surface but were uncommon underground.

SUBPLOT A.1.B: A three-story canopy kept this area well shaded with little or no direct sunlight reaching the surface (Figure 2). The

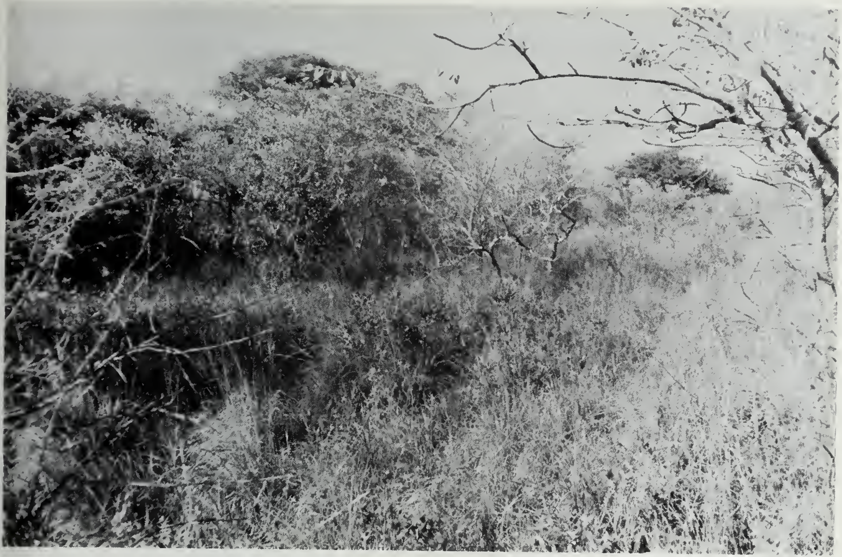
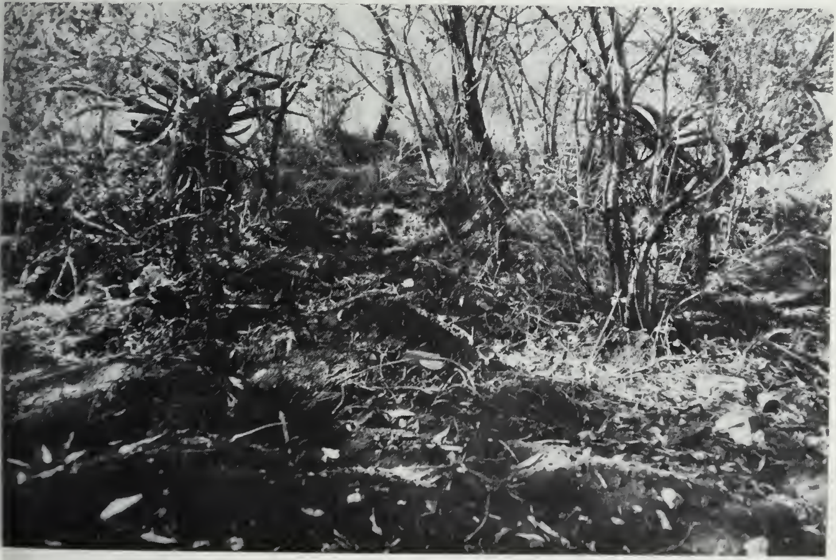


Fig. 1. Ndumu hill habitat in which Group A plots were located. This was the only area in which *Bufo regularis* was taken.



ig. 2. The A.1.b subplot after digging. It is still heavily shaded even though much of he understory vegetation was removed during the collecting.

ground cover was composed of the grasses *Trichoneura, Pogonarthria,* and *Aristida* and scattered small shrubs including *Maytenus senegalensis, Securinega virosa, Eugenia* sp., *Rhus guenzii, Euclea crispa,* and *Aloe marlothii.* The intermediate canopy was small trees reaching a height of 8 to 12 feet. These were *Vangueria cyanescens, Strychnos spinosa, Terminalia sericea, Boscia filipes, Dichrostachys cinerea,* and *Comniphora neglecta.* The upper canopy was a *Sclerocarya caffra* of up to 30 feet. The soil surface was covered by decomposing fruits of *Sclerocarya caffra,* leaf litter, and fragments of bark and twigs. The soil contained numerous roots but little other organic matter, and was damp to within 6 to 12 inches of the surface. Invertebrates were abundant throughout.

SUBPLOT A.1.C: This subplot had a discontinuous ground cover of the grasses *Trichoneura, Pogonarthria,* and *Aristida.* Some shading was provided by *Strychnos spinosa, Terminalia sericea,* and *Dichrostachys glomerata* up to 10 feet tall. The soil was dry to a depth of 15 to 18 inches, and contained clumps of matted grass roots, but few invertebrates.

PLOT A.2: This plot had an area of 55 square yards with red-brown soil rich in organic matter. It contained a single *Boscia* sp. 10 feet tall, *Aloe marlothii,* and isolated clumps of the grasses *Aristida* sp. and *Trichoneura* sp. The ground was covered by a 6-to-12-inch layer of decomposing plant material. There was abundant moisture at all depths and many invertebrates were present.

PLOT A.3: The plot consisted of 36 square yards of red-brown soil covered by a continuous layer of grasses (Figure 3). It was partly shaded by two *Kigelia pinata* 25 feet tall. The soil was dry to depths of 18 to 24 inches, and had clumps of grass roots and few invertebrates.

PLOT A.4: This area of 45 square yards of dark brown-gray soil was covered by a 2-foot layer of dried grass atop 6 inches of humus (Figure 4). The soil was loose, damp at all depths, and invertebrates were very abundant.

HABITAT GROUP B

The plots sampled were on the eastern slope of Ndumu hill bordering Khondo forest at an altitude of about 100 feet. The area is a sand forest bordering formerly cultivated fields. The ground cover in the forest included the shrubs *Salacia leptoclada, Vitex patula, Crassula* sp., *Jatropha variifolia, Sanseviera grandis, Senecio fulgens, Stylochiton natalense,* and *Ornithogalum virens.*

The soil surface was variously covered with both open and densely vegetated areas. The subordinate canopy was composed of 5-to-15-foot tall specimens of *Boscia longipedicillata, Wrightia natalensis,* and *Drypetes arguta.* The upper story of 15-30 foot trees included

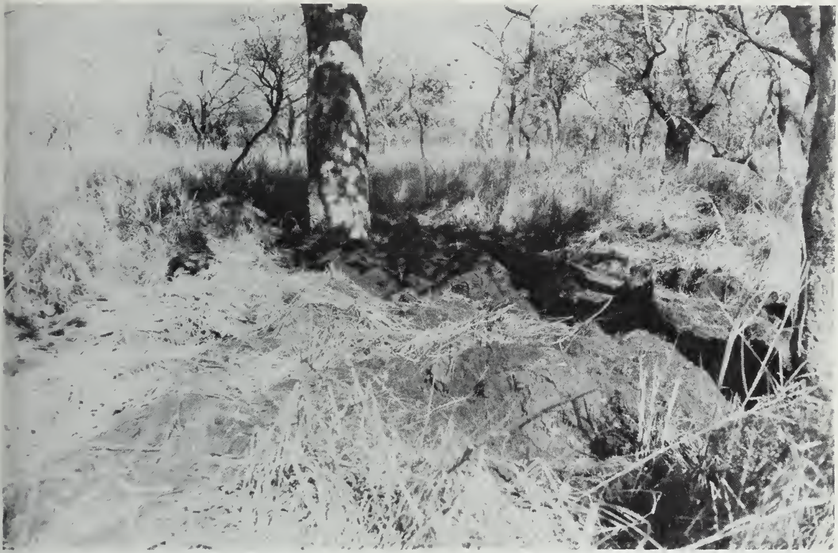


Fig. 3. Plot A.3 after digging was completed. The trees in the foreground are *Kigelia pinata* that partially shaded the collecting site.

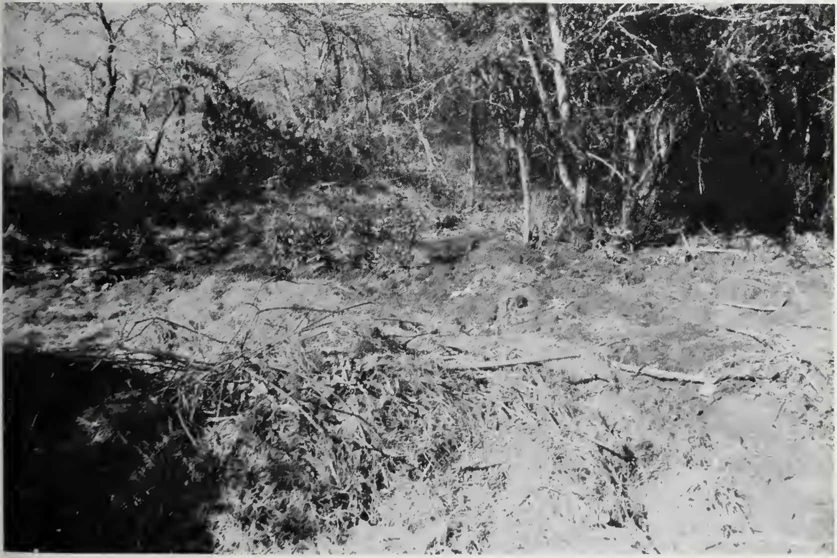


Fig. 4. The site of plot A.4. The remnants of dried grasses in the foreground originally covered the entire plot.

Cleistanthus schlechteri, Pteleopsis myrtifolia, Brachylaena huillensis, Croton gratissimus, and *Newtonia hildebrandtii,* which was the dominant species. The soil was fine, gray-white and contained some humus. All plots were 2 yards square.

plot b.1: This plot was in a densely shaded portion of the forest and was covered by a layer of leaf litter (Figure 5). The soil was moist to within 3 inches of the surface and contained many roots, bulbs, and invertebrates.

plot b.2: The plot was similar to B.1.

plot b.3: This plot lay at the base of a large specimen of *Albizza petersiana ssp. evansii* that was on the interface between forest and field. The plot was lightly shaded with a few clumps of small plants. The soil was fine, grayish-white in color. It was rich in organic matter, moist to within 3 inches of the surface but dry at the surface. Invertebrates were abundant.

plots b.4 and b.5: These plots were similar to B.3.

plot b.6: Specimens were collected from an area of short grass tufts at the edge of the forest. The soil was loose, moist below 3 inches, and had few invertebrates.

HABITAT GROUP C

These plots (2 square yards in area) were in old cultivated fields adjacent to the forest habitat in Group B (Figure 6). The area was formerly sand forest, and a few trees, e.g., *Sclerocarya caffra, Trichelia emetica, Acacia nilotica,* and *Gardenia cornuta* remained. A few *Maytenus heterophylla* bushes were present. The soil varied in color and texture, owing to erosion and repeated plowing. Subsoil invertebrates were uncommon.

plot c.1: This plot was in the center of an old field. Isolated tufts of grass were present. The orangish, fine, sandy soil was covered by leaf litter and twigs. Little organic matter was present and no invertebrates were observed.

plot c.2: This plot included an unused termite mound 3 feet tall. The mound was covered by *Azima tetracantha.* The mound was hard and dry at the surface but moist at a depth of 12 inches. The soil was orange-yellow, soft around the base of the mound, and rich in humus. No invertebrates were noted.

plot c.3: A plot at the base of a *Sclerocarya caffra* was sampled. It was lightly shaded and covered by a sparse layer of leaves and twigs. The soil was orange-yellow, dry at the surface, but moist at a depth of 12 inches. Few invertebrates were found.

Fig. 5. Site of plot B.1 after digging. A densely shaded area in the sand forest.

Fig. 6. View of old field area where Group C collections were made. Very few specimens were taken here.

PLOTS C.4 AND C.5: These plots were similar to C.3.

PLOT C.6: This plot was at the base of a *Trichelia emetica,* which provided dense shade. There was abundant leaf litter, and the brown soil was moist at all depths and rich in humus and invertebrates.

PLOT C.7: This plot was in the shade of a *Gardenia cornuta.* The area beneath a pile of leaves, grass, and twigs was sampled. Invertebrates were abundant.

PLOT C.8: This plot encompassed a small (1 m high), abandoned termite mound in open grassland. The soil was gray-brown, rich in humus, and contained little moisture. No invertebrates were noted.

HABITAT GROUP D

Twenty-six dams or pools were excavated at the base of Ndumu hill, on the edge of the Pongola River floodplain, at an elevation of 90 to 100 feet. The vegetation included the dominant grasses *Chloris virgata* and *Eragrostis cilianensis,* and the shrubs *Hermbstaedtia ordorata* and *Hibiscus cannabinus.* There were a few thickets of *Maytenus nemorosus* and some small trees like *Dichrostachys glomerata, Acacia nigrescens,* and *Acacia nilotica.* A few large trees, *Trichelia emetica, Sclerocarya caffra, Kigelia pinata,* provided shade in an otherwise open area. The soil was gray-black clay of extremely dense consistency. There were very few invertebrates.

SPECIES ABUNDANCE AND DISTRIBUTION

The species and numbers of individuals collected in 1970 are presented in Table 1. The species composition of the 1969 Ndumu hill collection is in Table 2. Since so few specimens of *Hemisus marmoratus* (1), *Xenocalamus transvaalensis* (1), *Aparallactus c. capensis* (1), *Scelotes arenicola* (2), and *Riopa sundevallii* (3) were collected, little may be said about their ecological distribution except that a variety of forms exists in a relatively small area at apparently low-population densities. Whether this reflects generally low incidence of these species in the area because of some adverse environmental factor, results from behavioral traits that cause wide dispersion, or is an artifact of the collecting technique, cannot be determined from these data.

Bufo regularis occurred only in Habitat Group A. This species was third in number of individuals collected. Since 7 specimens were taken in the Habitat A area and none in Habitat Groups B and C, it is probable that some environmental factor restricted their distribution.

Scelotes bidigittatus and *Zygaspis v. violacea* were by far the most abundant species. They made up 39% and 43%, respectively, and 82% collectively, of all specimens collected. All habitats sampled, with the exception of Group D, were occupied by these species.

TABLE 1. HABITAT

	GROUP A							GROUP B						
Species	A.1.a	A.1.b	A.1.c	A.2	A.3	A.4	Total	B.1	B.2	B.3	B.4	B.5	B.6	Total
Bufo regularis	1	2	0	1	0	3	7	0	0	0	0	0	0	0
Hemisus marmoratum	0	0	0	0	0	0	0	0	0	1	0	0	0	1
Riopa sundevallii	0	2	0	1	0	0	3	0	0	0	0	0	0	0
Scelotes bidigittatus	7	11	2	1	1	3	25	1	0	3	0	1	0	5
Scelotes arenicola	1	1	0	0	0	0	2	0	0	0	0	0	0	0
Zygaspis v. violacea	3	17	1	2	0	2	25	0	1	3	2	1	2	9
Aparallactus c. capensis	0	1	0	0	0	0	1	0	0	0	0	0	0	0
Xenocalamus transvaalensis	0	0	0	1	0	0	1	0	0	0	0	0	0	0
Total	12	34	3	6	1	8	64	1	1	7	2	2	2	15
Square Yards	120	120	120	55	36	45	496	2	2	2	2	2	2	12
Animals/Square Yard	.1	.28	.025	.019	.028	.178	.129	.5	.5	3.5	1.0	1.0	1.0	1.25

TABLE 1. HABITAT (continued)

Species	GROUP C									GROUP D		
	c.1	c.2	c.3	c.4	c.5	c.6	c.7	c.8	Total	D	Total	Total
Bufo regularis	0	0	0	0	0	0	0	0	0	0	0	7
Hemisus marmoratum	0	0	0	0	0	0	0	0	0	0	0	1
Riopa sundevallii	0	0	0	0	0	0	0	0	0	0	0	3
Scelotes bidigittatus	0	0	0	0	0	3	0	0	3	0	0	33
Scelotes arenicola	0	0	0	0	0	0	0	0	0	0	0	2
Zygaspis v. violacea	0	0	0	0	0	0	2	1	3	0	0	37
Aparallactus c. capensis	0	0	0	0	0	0	0	0	0	0	0	1
Xenocalamus transvaalensis	0	0	0	0	0	0	0	0	0	0	0	1
Total	0	0	0	0	0	3	2	1	6	0	0	85
Square Yards	2	2	2	2	2	2	2	2	16	?	?	524
Animals/Square Yard	0	0	0	0	0	1.5	1.0	.5	.375	0	0	.162

TABLE 2. NUMBERS OF SUBSOIL VERTEBRATES COLLECTED FROM NDUMUHILL IN 1969.

Scelotes bidigittatus	40
Scelotes arenicola	14
Zygaspis v. violacea	27
Riopa sundevallii	3
Aparallactus c. capensis	1
Atractaspis b. bibroni	2
Xenocalamus transvaalensis	1
Leptotyphlops conjuncta	3
Elapsoidea sundevallii decosteri	1
Calamelaps unicolor miolepis	1
Bufo regularis	7

HABITAT AND ECOLOGICAL FACTORS

Some caution must be applied in the interpretation of Table 1. The principal difficulty lies in comparison of the numbers of animals per square yard. The plots in Group A were much larger than those of Groups B and C. This may have biased the data since smaller plots were likely to be chosen to include optimal habitat areas while the larger plots of Group A contained areas of more varied habitat. Since amphisbaenians are well able to detect the vibrations caused by digging (Gans and Wever, 1972), there is a greater probability of escape from small than from large plots. Hence we have omitted statistical analyses until more comparable samples may be taken.

The relative abundance of invertebrates was the most obvious factor relating to the numbers of vertebrates present in the soil. When invertebrate abundance is categorized as either many or few, plots A.1.a, A.1.b, A.2, A.4, B.1, B.2, B.3, B.4, B.5, C.6, and C.7 had many, while A.1.c, A.3, B.6, C.1, C.2, C.3, C.4, C.5, and C.8 had few. In the 11 plots having many invertebrates, there were 78 vertebrates collected, compared with 7 from the 9 plots with few invertebrates. The number of vertebrates per square yard was .221 for the plots with many invertebrates, and was .041 for the plots with few invertebrates (Group D is omitted from this analysis). The correlation of abundant invertebrates and abundant reptiles does not appear in all the subgroups of A, confirming that other factors are also involved.

The next critical factor appears to be the particle size and packing of the soils (see Collis-George, 1959 for a theoretical discussion of soil environments). The area sampled for Group D was larger than the total of groups of A, B, and C, yet no specimens were collected. While no particle size analyses are available, inspection indicated that the relative proportion of fine, particulate silts is much higher in floodplain deposits than in the other sites. This is a well-known phenomenon reflecting the introduction of fine, particulate matter during flooding and its washing out by rainfall runoff from other areas. Equally important would seem to be the more ready drying and aeration in regions A, B, and C owing to wind action and root penetration.

All areas with high densities of invertebrate and vertebrate faunas represent natural associations. Group C, the old field habitat, had few invertebrates, a poor subsoil herpetofauna, and much tighter soil. This is of interest since certain other species of amphisbaenians, for instance *Amphisbaena schmidti, Amphisbaena caeca* (Gans, 1964), and *Cynisca leucura* (personal observation by Gans), are common in cultivated areas, particularly when the soils are well aerated. There seems to be an increase in invertebrates associated with monoculture. The present observations suggest that the suitability of once-cultivated areas may rapidly degenerate between the time cultivation ends and the time that natural vegetation is re-established. This could be of particular importance in tropical areas where soils are subject to rapid changes when even temporarily denuded of ground cover.

The effect of temporary flooding either by river water of by rain water should not be underestimated. Various central and east African regions are characterized by pans, localized zones in which the subsoil permeability has been reduced by particulates so that water remains standing for prolonged periods. Such pans attract game animals.

It is well known that when soil suspensions in water are allowed to settle, the largest particles settle first and fine, particulate matter then accumulates, forming a relatively fine-grained surface layer. It is this layer that presumably inhibits aeration in soil. Repeated flooding intensifies this process. Its results in nature may be seen in any small depression with poor drainage. A good example of such particulate stratification was observed (by Gans) along a transect bulldozed during road construction in the Tsavo National Park, Kenya. Each small depression showed the characteristic accumulation of fine, particulate matter as well as marked reduction in number and changes in the species composition of the fossorial vertebrates.

Finally, it might be useful to speculate briefly on the effect of the tunnel systems produced, at least by *Zygaspis,* on aeration and invertebrate distribution. Since the tunnels perforate the soil surface from below, they loosen the compacted layer and allow the finer particulates to drift downward. They serve as passageways for upward dispersion of water vapors. Laboratory observations suggest that they have a consequent attraction for hygrophilic insects. Besides providing access to food sources, they would facilitate vertical movements and act as sources and sinks for water and thermal energy. Unfortunately we still lack maps of even a few tunnel systems.

REFERENCES CITED

COLLIS-GEORGE, N.

1959. The physical environment of soil animals. Ecology, 40(4): 550-557.

GANS, CARL

1964. *Amphisbaena schmidti,* a third species of the genus from Puerto Rico (Amphisbaenia: Reptilia). (Notes on amphisbaenids No. 11). Breviora, (198): 1-11.

1968. Relative success of divergent pathways in amphisbaenian specialization. Amer. Nat., 102(926): 345-362.

1971. The amphisbaenians—enigmatic reptiles. African Wild Life, 24(4): 277-281.

GANS, CARL, AND ERNEST GLEN WEVER

1972. The ear and hearing in Amphisbaenia (Reptilia). Jour. Exper. Zool, 179(1): 17-34.

NUTTONSON, M. Y.

1961. The physical environment and agriculture of South Africa with special reference to its winter-rainfall regions containing areas climatically and latitudinally analogous to Israel. Washington, D.C., American Institute of Crop Ecology, 459 pp.

POOLEY, A. C.
1965. A preliminary check-list of the reptiles found within the Mkuzi and Ndumu Game Reserve in Northern Zululand. Lammergeyer, 3(2): 41-55.
1970. Additional reptile records for the Ndumu Game Reserve in Northern Zululand. Lammergeyer, (11): 65-67.
STUCKENBERG, B. R.
1969. Effective temperature as an ecological factor in Southern Africa. Zoologica Africana, 4(2): 145-197.

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CATALOGUE OF THE GENERA OF DINOSAURS

THEODORE E. WHITE[1]

When I assumed my duties at Dinosaur National Monument in September, 1953, I realized that many of the genera of dinosaurs, possibly fifty percent, were founded on very fragmentary material and could not be considered valid. In order to form an opinion regarding the validity of a particular genus it was necessary to have a statement of the material upon which it was founded. I needed this information on all the described genera of dinosaurs. Since no such list was available it was necessary to prepare one. I used the list of genera in the *Osteology of the Reptiles,* by A. S. Romer, and entered them on 3″ x 5″ cards. On each card I listed the genus, author, and year; the family and suborder to which the genus belonged; the type species; the elements of which the type specimen consisted; and the horizon and locality of the type specimen. When data were available, I included the catalogue number of the type specimen and the museum in which it was located, or both.

My comment on the validity of each generic name in the alphabetical list appears in brackets.

Such a listing of the genera of dinosaurs should follow the system of classification with which most students are familiar, and I accordingly used the classification of the dinosaurs in *Osteology of the Reptiles,* by A. S. Romer. This is a conservative classification and does not reflect the current thought of many students of dinosaurs, particularly in regard to the Theropoda and Sauropoda. It will be several years, however, before the new ideas on these two groups can be fully developed and incorporated into a relatively stable classification.

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I have not included references to the original description of each genus because this information is available in the bibliographies of Hay, Camp *et al;* Romer *et al,* Fossilium Catalogues, and the Zoological Record. The inclusion of this information would have needlessly increased the bulk of the manuscript. I have not listed the author of the species when it was the same as that of the genus.

The preparation of this catalogue has revealed the complete absence of sauropods on the North American continent prior to Morrison (Kimeridgean) time. They suddenly appeared in the Morrison sediments in considerable number and variety and are unknown in the older sediments. Sauropods were present in Europe and South America during the Medial Jurassic, and in India, South Africa, and Australia during the Early Jurassic. Land traffic was not possible between Asia and North America during the Early and Medial Jurassic, but became possible at the beginning of Morrison time. Therefore, it is necessary to postulate a mass immigration over the Chukchi-Alaska land bridge with the advent of Morrison time. This explanation would appear to apply to *Stegosaurus,* also.

I am indebted to Dr. John Ostrom of Yale, Dr. John McIntosh of Wesleyan University, Mr. Gilbert Stucker of the American Museum of Natural History, Dr. Alan Charig of the British Museum (Natural History), and Dr. Joseph Gregory and Mr. Robert Long of the University of California for furnishing information on a number of type specimens. I am also indebted to Dr. Nicholas Hotton III for the loan of literature and information on type specimens.

ABBREVIATION OF MUSEUM NAMES

AC	Amherst College
AMNH	American Museum of Natural History
ANSP	Academy of Natural Sciences of Philadelphia
BMNH	British Museum (Natural History)
CUP	Catholic University, Peking
CM	Carnegie Museum
EM	Elgin Museum, Elgin, Scotland
FM	Field Museum, Chicago
GSC	Geological Survey of Canada
IM	Indian Museum, Calcutta
IPHG	Institute für Paläontologie und historische Geologie, Munich
IRSNB	Institute Royal de Sciences Naturelle de Belgique
IVP AS	Institute of Vertebrate Paleontology, Academia Sinica, Peking
LVP GSC	Laboratory of Vertebrate Paleontology, Geological Survey of China
MCZ	Museum of Comparative Zoology
MIWG	Museum Isle of Wight Geology

MLP	Museo de La Plata
MNHN	Muséum National d' Histoire Naturelle, Paris
MUO	Stovall Museum of Science and History, University of Oklahoma
NMC	National Museum of Canada
PEN AN SSR	Paleontological Institute, Academy of Science, USSR
PVL	Paleontología Vertebrados Lillo, Argentina
RCS	Royal College of Surgeons, London
ROM	Royal Ontario Museum
SAFM	South African Museum
SM	Sedgwick Museum, Cambridge
SMNS	Staatliches Museum für Naturkunde, Stuttgart
TRM	Transvaal Museum
UCMP	University of California Museum of Paleontology
UKMNH	University of Kansas Museum of Natural History
UMMP	University of Michigan Museum of Paleontology
UMO	University Museum, Oxford
USNM	United States National Museum
YPM	Yale Peabody Museum

ALPHABETICAL LISTING OF GENERA

Acanthopholis Huxley, 1867
Acanthopholidae, Ankylosauria
[valid]
Genotype: *horridus.*
Type: Occiput, 3 teeth, distal end of humerus, vertebral centra, numerous armour plates. Mus. Pract. Geol., London.
Lower Cretaceous, Greensand—Europe, England, Cambridge, Folkstone.

Acrocanthosaurus Stovall and Langston, 1950
Megalosauridae, Carnosauria
[valid]
Genotype: *atokensis.*
Type: Partial skull and partial skeleton. MUO 8-0-59.
Lower Cretaceous, Trinity Sands—North America, Oklahoma, Atoka County.

Aegyptosaurus Stromer, 1932
Diplodocidae, Sauropoda
[valid]
Genotype: *baharijensis.*
Type: Left scapula, left humerus, left radius, right ulna, left femur, left tibia. Probably destroyed. Not at IPHG.
Upper Cretaceous, Lower Cenomanian—North Africa, Egypt, Baharije.

Aepisaurus Gervais, 1853
Diplodocidae, Sauropoda [*nomen dubium*]
Genotype: *elephantinus.*
Type: Humerus. MNHN.
Lower Cretaceous, Aptian—Europe, France, Dept. Vaucluse, Monte Ventoux.

Aepyosaurus Huene, 1932
Diplodocidae, Sauropoda
[mispelling of *Aepisaurus.*]

Aetonyx Broom, 1911
Thecodontosauridae, Prosauropoda
[valid]
Genotype: *palustris.*
Type: Scapula, coracoid, humerus, radius, part of ulna, manus, proximal end of tibia, pes. SAFM 2769, 2770.
Upper Triassic, Stormberg Series, Top of Red Beds—South Africa, Orange Free State, Fouriesburg.

Agathaumas Cope, 1872
Ceratopsidae, Ceratopsia
[*nomen dubium*]
Genotype: *sylvestris.*
Type: Right ilium, 9 posterior dorsal and sacral centra. AMNH 4000.

Upper Cretaceous, Lance Formation—North America, Wyoming, Sweetwater County, Black Buttes.

Aggiosaurus Ambayrac, 1913
Megalosauridae, Carnosauria
[=*Megalosaurus fide* Romer 1956]
Genotype: *nicaeensis.*
Type: Lower jaw.
Upper Jurassic, Oxfordian—Europe, France, Cap-d' Ail a' la Turbie.

Agrosaurus Seeley, 1891
Coeluridae, Coelurosauria
[provisionally considered valid]
Genotype: *macgillivrayi.*
Type: Left tibia, proximal end of right tibia, distal end of right radius, claw and broken tooth. BMNH 49984.
Lower Jurassic—Australia, Queensland, York Peninsula.

Alamosaurus Gilmore, 1922
Diplodocidae, Sauropoda
[valid]
Genotype: *sanjuanensis.*
Type: Left scapula. USNM 10,486.
Upper Cretaceous, Ojo Alamo Formation—North America, New Mexico, San Juan County, 1 mi. south of Ojo Alamo.

Albertosaurus Osborn, 1905
Tyrannosauridae, Carnosauria
[valid]
Genotype: *sarcophagus.*
Type: Palatal region of skull, brain case, and lower jaws. NMC 5600.
Upper Cretaceous, Edmonton Formation, Member A—North America, Alberta, Red Deer River, Knee Hills Creek.

Alectrosaurus Gilmore, 1933
Tyrannosauridae, Carnosauria
[valid]
Genotype: *olseni.*
Type: Right humerus, part of manus, femur, tibia, fibula, and pes. AMNH 6368.
Upper Cretaceous, Iren Dabasu Formation—East Asia, Mongolia, Iren Dabasu telegraph station.

Algoasaurus Broom, 1904
Diplodocidae, Sauropoda
[valid]
Genotype: *bauri.*
Type: Fragmentary vertebrae, femur, imperfect scapula, phalanx. Port Elizabeth Museum.
Lower Cretaceous, Sunday River Formation—South Africa, Uitenhage.

Allosaurus Marsh, 1877
Megalosauridae, Carnosauria
[*nomen dubium*]
Genotype: *fragilis.*
Type: One tooth, 2 dorsal centra, proximal phalanx of digit 3 of right pes. YPM 1930.
Upper Jurassic, Morrison Formation—North America, Colorado, Fremont County, Garden Park, Sec. 28, T. 17S, R. 70W.

Altispinax Huene, 1923
Megalosauridae, Carnosauria
[*nomen dubium*]
Genotype: *dunkeri* Dames, 1884.
Type: Worn tooth. University of Marburg collection.
Lower Cretaceous, Wealden Formation—Europe, Belgium, Hanover, Deister.

Ammosaurus Marsh, 1891
Ammosauridae, Coelurosauria
[valid]
Genotype: *major* Marsh, 1889.
Type: Three presacral vertebrae, sacrum, pelvis, both hind legs and pedes. YPM 208.
Upper Triassic, Newark Series, Portland Sandstone—North America, Connecticut, Hartford County, Manchester.

Amphicoelias Cope, 1877
Diplodocidae, Sauropoda
[*nomen dubium*]
Genotype: *altus.*
Type: Two imperfect dorsal vertebrae, femur, scapula, coracoid, ulna, AMNH 5764.
Upper Jurassic, Morrison Formation—North America, Colorado, Fremont County, Garden Park.

Amphisaurus Marsh, 1882
Anchisauridae, Prosauropoda
[preoccupied=*Anchisaurus* Marsh, 1885]
Genotype: *polyzelus* Hitchcock, 1865.
Type: One dorsal and four caudal vertebrae, distal ends of right radius and ulna, right manus, two ischia, left femur, proximal end of tibia, left

fibula and pes. AC 41/109-118.
Upper Triassic, Newark Series, Longmeadow Sandstone—North America, Massachusetts, Hampden County, Springfield.

Amygdalodon Cabrera, 1947
Camarasauridae, Sauropoda
[valid]
Genotype: *patagonicus.*
Type: Several vertebrae, partial scapula, partial pubis, four teeth. MLP 46-VIII-21-1.
Medial Jurassic, Bajocian—South America, Argentina, Chubut province, Pampa de Agnia.

Anatosaurus Lull and Wright, 1942
Hadrosauridae, Ornithopoda
[valid]
Genotype: *annectens* Marsh, 1892.
Type: Skull and skeleton. USNM 2414.
Upper Cretaceous, Lance Formation—North America, Wyoming, Niobrara County, Lightning Creek.

Anchiceratops Brown, 1914
Ceratopsidae, Ceratopsia
[valid]
Genotype: *ornatus.*
Type: Skull with anterior end missing. AMNH 5251.
Upper Cretaceous, Edmonton Formation, Member B—North America, Alberta, Tolman Ferry.

Anchisaurus Marsh, 1885
Anchisauridae, Prosauropoda
[valid]
Genotype: *polyzelus* Hitchcock, 1865.
Type: One dorsal and four caudal vertebrae, right manus, distal ends of right radius and ulna, left femur, proximal end of left tibia, left fibula and pes, two ischia. AC 41/109-118.
Upper Triassic, Newark Series, Longmeadow Sandstone—North America, Massachusetts, Hampden County, Springfield.

Ankylosaurus Brown, 1908
Ankylosauridae, Ankylosauria
[valid]
Genotype: *magniventris.*
Type: Skull, scapula-coracoid, seven cervical, ten dorsal, and four caudal vertebrae, ribs and dermal plates. AMNH 5895.
Upper Cretaceous, Hell Creek Beds—North America, Montana, Valley County, 120 miles N. of Miles City.

Anodontosaurus Sternberg, 1929
Nodosauridae, Ankylosauria
[valid]
Genotype: *lambei.*
Type: Skull, left jaw, many dermal plates. NMC 8530.
Upper Cretaceous, Edmonton Formation, Member A—North America, Alberta, Red Deer River, Morrin.

Anoplosaurus Seeley, 1879
Iguanodontidae, Ornithopoda
[*nomen dubium*]
Genotype: *curtonotus.*
Type: Six cervical, twelve dorsal, six sacral, and eight caudal centra, parts of both coracoids, proximal end of scapula, proximal and distal ends of humerus. SM.
Lower Cretaceous, Greensand—Europe, England, Cambridge.

Antarctosaurus Huene, 1929
Diplodocidae, Sauropoda
[valid]
Genotype: *wichmannianus*
Type: Skull, one cervical vertebra, scapula, radius, ulna, manus, pelvis, hind leg. MLP.
Upper Cretaceous, Upper Senonian—South America, Argentina, Rio Negro, General Roca.
Remarks: The family or subfamily to include the Cretaceous peg-toothed sauropods with procoelus caudal vertebrae should be based upon this genus because it would then be capable of definition. More will be said on this under *Titanosaurus.*

Antrodemus Leidy, 1870
Megalosauridae, Carnosauria
[valid]
Genotype: *valens.*
Type: Posterior half of sixth caudal vertebra. USNM 218.
Neotype: Skeleton, USNM 8367.
Upper Jurassic, Morrison Formation—North America, Colorado, Grand County, Middle Park.

Apatosaurus Marsh, 1877
Camarasauridae, Sauropoda
[valid]
Genotype: *ajax.*
Type: Most of skeleton with brain case, YPM 1860.
Upper Jurassic, Morrison Formation—North America, Colorado, Jefferson County, Morrison, Sec. 35, T. 4S, R. 70W.

Aralosaurus Rozhdestvensky, 1970
Hadrosauridae, Ornithopoda
[valid]
Genotype: *tuberiferus.*
Type: Incomplete skull; PEN AN SSR 2229/1.
Lower portion of Upper Cretaceous—Central Asia, central Kazakhstan, n. of Karmakchi (Dzhusaly Station), Beleutinskaia suite.

Archaeornithomimus Russell, 1972
Ornithomimidae, Coelurosauria
[valid]
Genotype: *asiaticus,* Gilmore, 1933.
Type: Gilmore (1933:27) designates two cotypes: AMNH 6565 including much of pes, and AMNH 6569, representing a nearly complete manus.
Upper Cretaceous, Cenomanian?, Iren Dabasu Formation—East Asia, Mongolia, Gobi Desert, 8 mi. e. of Iren Dabasu telegraph station.

Arctosaurus Adams, 1875
Thecodontosauridae, Prosauropoda
[*nomen dubium* (probably Chelonian, *fide* Huene, 1906)]
Genotype: *osborni.*
Type: Most of a cervical vertebra. Mus. Sci. and Art, Dublin.
Upper Triassic, Heiberg Formation—North America, Arctic Archipelago, Bathurst Group, Cameron Island.

Argyrosaurus Lydekker, 1893
Diplodocidae, Sauropoda
[valid]
Genotype: *superbus.*
Type: Left front leg and manus. MLP.
Upper Cretaceous, Upper Senonian—South America, Argentina Chubut province, Rio Chico.

Aristosaurus van Hoepen, 1920
Thecodontosauridae, Prosauropoda
[= *Gyposaurus, fide* Romer, 1956]
Genotype: *erectus.*
Type: Skull and most of skeleton. TrM.
Upper Triassic, Stormberg Series, bottom of Cave Sandstone—South Africa, Orange Free State, Rosendal.

Aristosuchus Seeley, 1887
Coeluridae, Coelurosauria
[provisionally considered valid]
Genotype: *pusillus* Owen, 1876.
Type: Five lumbo-sacral vertebrae, 2 pubes. BMNH R178.
Lower Cretaceous, Wealden—Europe, England, Isle of Wight, Brook.

Arrhinoceratops Parks, 1925
Ceratopsidae, Ceratopsia
[valid]
Genotype: *brachyops.*
Type: Skull without jaws. ROM 796.
Upper Cretaceous, Edmonton Formation, Member A—North America, Alberta, Bleriot Ferry.

Asiatosaurus Osborn, 1924
Camarasauridae, Sauropoda
[*nomen dubium*]
Genotype: *mongoliensis.*
Type: A single tooth. AMNH 6264.
Lower Cretaceous, Oshih Formation—East Asia, Mongolia, Oshih.

Astrodon Johnston, 1859
Camarasauridae, Sauropoda
[*nomen dubium*]
Genotype: johnstoni Leidy, 1865.
Type: One tooth. YPM 798.
Lower Cretaceous, Arundel Formation—North America, Maryland, Prince Georges County, Swampoodle.

Atlantosaurus Marsh, 1877
Camarasauridae, Sauropoda
[*nomen dubium*]
Genotype: *montanus.*
Type: Incomplete sacrum. YPM 1835.
Upper Jurassic, Morrison Formation—North America, Colorado, Jefferson County, Morrison Sec. 26, T. 4S, R. 70W.

Aublysodon Leidy, 1868
Tyrannosauridae, Carnosauria
[*nomen dubium*]

Genotype: *mirandus*.
Type: Several teeth from the type series of *Deinodon*. ANSP.
Upper Cretaceous, Judith River Beds—North America, Montana, Chouteau County, Fort Benton.

Austrosaurus Longman, 1933
Cetiosauridae, Sauropoda
[*nomen dubium*]
Genotype: *mckillopi*.
Type: Six imperfect dorsal vertebrae. Queensland Museum. F2316.
Lower Cretaceous, Tambo Series (Albian)—Australia, Queensland, Clutha.

Avalonia Seeley, 1898
Melanorosauridae, Prosauropoda
[preoccupied, Walcott, 1889, =*Avalonianus* Kuhn, 1961]

Avalonianus Kuhn, 1961
Melanorosauridae, Prosauropoda
[*nomen dubium*]
Genotype: *sanfordi* Seeley, 1898.
Type: A single tooth. BMNH R2869.
Upper Triassic, Rhaetic—Europe, England, Somerset, Wedmore Hill.

Avipes Huene, 1932
Podokesauridae, Coelurosauria
[provisionally considered valid]
Genotype: *dillstedianus*.
Type: Three incomplete metatarsals. Preussische Geologische Landesanstalt, Berlin.
Middle Triassic, Lettenkohle—Europe, Germany, Thuringia.

Bactrosaurus Gilmore, 1933
Hadrosauridae, Ornithopoda
[valid]
Genotype: *johnsoni*.
Type: Partial skull, ten dorsal, seven sacral and 36 caudal vertebrae, left scapula, left sternum, both pubes and ischia, left femur, fibula and pes. AMNH 6553.
Upper Cretaceous, Iren Dabasu Formation—East Asia, Mongolia, Iren Dabasu.

Bahariasaurus Stromer, 1934
Megalosauridae, Carnosauria
[provisionally considered valid]
Genotype: *ingens*.
Type: Two pubes, one ischium, two dorsal and three sacral vertebrae. Probably destroyed. Not at IPHG.
Upper Cretaceous, Lower Cenomanian—North Africa, Egypt, Baharije Basin.

Barosaurus Marsh, 1890
Diplodocidae, Sauropoda
[valid]
Genotype: *lentus*.
Type: Four cervical, six dorsal, and 19 caudal vertebrae, sacrum, one sternal plate, one scapula, ilium, pubis, ischium, fragments of femur, tibia and fibula. YPM 429.
Upper Jurassic, Morrison Formation—North America, South Dakota, Meade County, Piedmont, Black Hills.

Basutodon Huene, 1932
Teratosauridae, Carnosauria
[*nomen dubium*]
Genotype: *ferox*.
Type: A single tooth. National Museum, Bloemfontein.
Upper Triassic, Stormberg Series, Red Beds—South Africa, Basutoland, Lesotho.

Betasuchus Huene, 1932
Ornithomimidae, Coelurosauria
[*nomen vanum fide* D. Russell, 1970]
Genotype: *bredai*.
Type: Femur. BMNH 32997.
Upper Cretaceous, Upper Senonian—Europe, Holland, Maastricht.

Bothriospondylus Owen, 1875
Cetiosauridae, Sauropoda
[*nomen dubium*]
Genotype: *suffosus*.
Type: Centra of four dorsal vertebrae, BMNH 44592-5, and three sacral vertebrae, BMNH 44589-91.
Upper Jurassic, Kimeridgean, Kimeridge Clay—Europe, England, Wiltshire, Swindon.

Brachiosaurus Riggs, 1903
Cetiosauridae, Sauropoda
[valid]
Genotype: *altithorax*.
Type: Sacrum, seven presacral and two anterior caudal vertebrae, right humerus, coracoid and femur. FM.
Upper Jurassic, Morrison Formation—North America, Colorado, Mesa County, Fruita.

Brachyceratops Gilmore, 1914
Protoceratopsidae, Ceratopsia
[*Centrosauras* fide Sternberg, 1940. (young animal]
Genotype: *montanensis.*
Type: Considerable portion of a disarticulated skull, right dentary and predentary. USNM 7951.
Upper Cretaceous, Two Medicine Formation—North America, Montana, Glacier County.

Brachylophosaurus Sternberg, 1953
Hadrosauridae, Ornithopoda
[valid]
Genotype: *canadensis.*
Type: Skull, jaws, cervical and dorsal vertebrae, two scapulae, two coracoids, two front legs. NMC 8893.
Upper Cretaceous, Belly River Series, Oldman Formation—North America, Alberta, Red Deer River, Little Sandhill Creek.

Brachypodosaurus Chakravarti, 1934
Nodosauridae, Ankylosauria
[provisionally considered valid]
Genotype: *gravis.*
Type: Humerus. IM.
Upper Cretaceous, Lameta Beds—South Asia, India, Jubbulpure.

Brasileosaurus Huene, 1931
Compsognathidae, Coelurosauria
[problematic, also referred to Crocodilia]
Genotype: *pachecoi.*
Type: Information not available.
Lower Cretaceous, Lower Senonian—South America, Brazil.

Brontosaurus Marsh, 1879
Camarasauridae, Sauropoda
[=*Apatosaurus, fide* Riggs, 1903]
Genotype: *excelsus.*
Type: Skeleton lacking skull. YPM 1980.
Upper Jurassic, Morrison Formation—North America, Wyoming, Como Bluff, Quarry 10, Sec. 12, T. 22N, R. 77W.

Remarks: The type of *Brontosaurus* has the muscle scars clearly defined by exostosis. The type of *Apatosaurus* is a young animal but it is still twenty-five percent larger than *Brontosaurus.* Both types should be thoroughly restudied and Riggs determination re-evaluated.

Caenognathus Sternberg, R. M., 1940
Caenognathidae, Coelurosauria
[valid]
Genotype: *collinsi.*
Type: Lower jaws. GSC 8776.
Upper Cretaceous, Belly River Series, Oldman Formation—North America, Alberta, Steveville, Sand Creek.
Remarks: This specimen was originally described as a toothless bird, but the leading ornithologists have returned it to the Reptilia. It has recently been returned to the birds (*fide* Cracraft, 1971).

Calamosaurus Lydekker, 1891
Coeluridae, Coelurosauria
[=*Calamospondylus*=*nomen dubium*]
Genotype: *foxi.*
Type: Two cervical vertebrae. BMNH R901.
Lower Cretaceous, Wealden—Europe, England, Isle of Wight.

Calamospondylus Lydekker, 1889
Coeluridae, Coelurosauria
[*nomen dubium*]
Genotype: *foxi.*
Type: Two cervical vertebrae. BMNH R901.
Lower Cretaceous, Wealden—Europe, England, Isle of Wight.

Camarasaurus Cope, 1877
Camarasauridae, Sauropoda
[valid]
Genotype: *supremus.*
Type: One cervical, three dorsal, and four caudal vertebrae, AMNH 5760.
Upper Jurassic, Morrison Formation—North America, Colorado, Fremont County, Canyon City, Garden Park.
Remarks: The family *Camarasauridae* was established by Cope in 1877 and the genus remains the best known among spatulate-toothed sauropods. Our knowledge of this genus is based upon the wealth of material associated with the type and three skeletons of *Camarasaurus lentus* Marsh. *Camarasauridae* should be used instead of *Brachiosauridae.*

Camptonodus Hoffman, 1880
Iguanodontidae, Ornithopoda
[mispelling of *Camptonotus*= *Camptosaurus*]

Camptonotus Marsh, 1879
Iguanodontidae, Ornithopoda
[preoccupied=*Camptosaurus* Marsh, 1885]

Camptosaurus Marsh, 1885
Iguanodontidae, Ornithopoda
[valid]
Genotype: *dispar* Marsh, 1879.
Type: Seven cervical and first dorsal vertebrae, both femura, tibia, fibula, pes and manus. YPM 1877.
Upper Jurassic, Morrison Formation—North America, Wyoming, Como Bluff, Quarry 13, Sec. 4, T. 22N, R. 77W.

Campylodon Huene, 1929
Camarasauridae, Sauropoda
[preoccupied=*Campylodoniscus* Kuhn, 1961]

Campylodoniscus Kuhn, 1961
Camarasauridae, Sauropoda
[valid—to replace Campylodon Huene, 1929.]
Genotype: *ameghinoi* Huene, 1929.
Type: Left maxilla with one tooth. MLP.
Upper Cretaceous, Coniacian—South America, Argentina, Chubut, Sierra San Bernardo.

Carchrodontosaurus Stromer, 1931
Megalosauridae, Carnosauria
[provisionally considered valid].
Genotype: *saharicus* Depéret et Savarnin, 1927.
Type: Two teeth.
Lower Cretaceous, Albian—North Africa, Algiers, Timiumoun.
Remarks: Stromer had skull fragments and other bones from Baharije.

Cardiodon Owen, 1841
Cetiosauridae, Sauropoda
[*nomen dubium*]
Genotype: *rugulosus.*
Type: One tooth. BMNH R1527.
Middle Jurassic, Upper Bathonian, Forest Marble—Europe, England, Wiltshire, Bradford.

Caudocoelus Huene, 1932
Coeluridae, Coelurosauria
[*nomen dubium*]
Genotype: *sauvagei.*
Type: One distal caudal vertebra. Destroyed.
Upper Jurassic, Kimeridgean—Europe, France, Boulogne.

Caulodon Cope, 1877
Camarasauridae, Sauropoda
[=*Camarasaurus fide* White, 1958]
Genotype: *diversidens.*
Type: Ten teeth. AMNH 5768.
Upper Jurassic, Morrison Formation—North America, Colorado, Fremont County, Canyon City, Garden Park.

Centrosaurus Lambe, 1904
Ceratopsidae, Ceratopsia
[valid]
Genotype: *apertus.*
Type: Posterior crest. NMC 971.
Upper Cretaceous, Belly River Series—North America, Alberta, Steveville.

Cetiosauriscus Huene, 1929
Cetiosauridae, Sauropoda
[=*Cetiosaurus fide* Romer, 1956]
Genotype: *leedsi* Hulke, 1877.
Type: Pelvis. BMNH R3078.
Upper Jurassic, Oxfordian, Oxford Clay—Europe, England, Peterborough.

Cetiosaurus Owen, 1841
Cetiosauridae, Sauropoda
[valid]
Genotype: *oxoniensis* Phillips, 1871.
Type: Much of skeleton. UMO.
Middle Jurassic, Bathonian, Great Oolite—Europe, England, Oxfordshire, Enslow.
Remarks: Apparently Owen did not designate a type species for this genus. In 1888 Lydekker designated *oxoniensis* Phillips, 1871 as the type species and in the absence of earlier designated types this must stand. After these many years the type of *Cetiosaurus oxoniensis* should be restudied and compared with the corresponding bones of *Haplocanthosaurus.* It is entirely possible that the two are congeneric.

Ceratops Marsh, 1888
Ceratopsidae, Ceratopsia

[*nomen dubium fide* Lull, 1933]
Genotype: *montanus.*
Type: Occipital condyle and a pair of frontal horns. USNM 2411.
Upper Cretaceous, Judith River Formation—North America, Montana, Fergus County, Cow Creek.

Ceratosaurus Marsh, 1884
Megalosauridae, Carnosauria
[valid]
Genotype: *nasicornis.*
Type: Nearly entire skeleton with skull. USNM 4735.
Upper Jurassic, Morrison Formation—North America, Colorado, Fremont County, Canyon City, Garden Park, Sec. 28, T. 17S, R. 70 W.

Chasmosaurus Lambe, 1914
Ceratopsidae, Ceratopsia
[valid]
Genotype: *belli.*
Type: Coalesced parietals. GSC 491.
Upper Cretaceous, Belly River Series—North America, Alberta, Red Deer River, Steveville.

Cheneosaurus Lambe, 1917
Hadrosauridae, Ornithopoda
[valid]
Genotype: *tolmanensis.*
Type: Skull, limb bones, pelvic arch, and vertebrae. NMC 2246.
Upper Cretaceous, Edmonton Formation, Member B—North America, Alberta, Red Deer River, Tolman Ferry.

Chialingosaurus Young, 1959
Stegosauridae, Stegosauria
[valid]
Genotype: *kuani.*
Type: Six vertebrae, three spines, two coracoids, two humeri, one radius, part of ischium, one femur. IVP AS V2300.
Upper Jurassic—East Asia, China, Szechuan, 200 km. N of Chungking.

Chiayusaurus Bohlin, 1953
Camarasauridae, Sauropoda
[*nomen dubium*]
Genotype: *lacustris.*
Type: Posterior tooth.
Upper Cretaceous, Djadocta equivalent—East Asia, China, W. Kansu, Chia-Yü-Kuan.

Chienkosaurus Young, 1942
Megalosauridae, Carnosauria
[*nomen dubium*]
Genotype: *ceratosauroides.*
Type: Four isolated teeth. IVP AS V237.
Upper Jurassic—East Asia, China, N. Szechuan, Kuangyuan.

Chilantaisaurus Hu, 1964
Megalosauridae, Carnosauria
[valid]
Genotype: *tashnikouensis.*
Type: Right humerus, ungual phalanx, fragmentary ilium, two femora, right fibuls, right metatarsals 2, 3, and 4, left metatarsals 3 and 4. IVP AS 2884.
Upper Cretaceous—East Asia, Inner Mongolia, Tashnikou, Chilantai, Alashan.

Chingkankousaurus Young, 1958
Tyrannosauridae, Carnosauria
[provisionally considered valid]
Genotype: *fragilis.*
Type: Right scapula. IVP AS 636.
Upper Cretaceous, Wangshih Series—East Asia, China, Shantung, Laiyang Basin.

Chirostenotes Gilmore, 1924
Dromaeosauridae, Coelurosauria
[valid]
Genotype: *pergracilis.*
Type: Right and left manus nearly complete. NMC 2367.
Upper Cretaceous, Belly River Series, Oldman Formation—North America, Alberta, Steveville, Little Sandhill Creek.

Chondrosteosaurus Owen, 1876
Cetiosauridae, Sauropoda
[*nomen dubium*]
Genotype: *gigas.*
Type: Two centra of posterior cervical vertebrae, BMNH 46869 and 46870.
Lower Cretaceous, Wealden—Europe, England, Isle of Wight (south shore).

Cinodon Cope, 1874
Hadrosauridae, Ornithopoda
[misspelling of *Cionodon*=*nomen dubium*]

Cionodon Cope, 1874
Hadrosauridae, Ornithopoda
[*nomen dubium fide* Lull and Wright, 1942]
Genotype: *arctatus.*
Type: Portion of right maxilla, two dorsal vertebrae, distal end of metatarsal, distal end of ulna. AMNH 3951.
Upper Cretaceous, Denver Formation—North America, Colorado, Lodge Pole Creek.

Clarencea Brink, 1959
Ornithosuchidae, Carnosauria
[valid]
Genotype: *gracilis.*
Type: Information not available. Bernard Price Institute 288.
Upper Triassic, Stormberg Series, Red Beds—South Africa.

Clarenceia Brink, 1959
Ornithosuchidae, Carnosauria
[=*Clarencea* Brink]

Cladeiodon Owen, 1841
Teratosauridae, Carnosauria
[*nomen dubium*]
Genotype: *lloydii.*
Type: A single tooth. Apparently lost.
Upper Triassic, Warwickshire Sandstone—Europe, England, Warwickshire, Cotton End Quarry.

Claderodon Agassiz, 1846
Teratosauridae, Carnosauria
[misspelling of *Cladeiodon* Owen, 1841]

Cladyodon Owen, 1842
Teratosauridae, Carnosauria
[misspelling of *Cladeiodon* Owen, 1841]

Claorhynchus Cope, 1892
Hadrosauridae, Ornithopoda
[*nomen dubium fide* Lull and Wright, 1942]
Genotype: *trihedrus.*
Type: Premaxillary tip and predentary. AMNH 3978.
Upper Cretaceous, Judith River Formation—North America, Montana, Fergus County, Judith River.

Claosaurus Marsh, 1890
Hadrosauridae, Ornithopoda
[valid]
Genotype: *agilis* Marsh, 1872.
Type: Skeleton with partial skull. YPM 1190.
Upper Cretaceous, Niobrara Formation—North America, Kansas, Smoky Hill River.

Clasmodosaurus Ameghino, 1899
Megalosauridae, Carnosauria
[*nomen dubium*]
Genotype: *spatula.*
Type: Three teeth. MLP.
Upper Cretaceous, Upper Senonian—South America, Argentina, Santa Cruz, Rio Sehuen.

Coelophysis Cope, 1889
Podokesauridae, Coelurosauria
[valid]
Genotype: *bauri* Cope, 1887.
Type: Ilium, sacrum, several vertebrae, supplemented by twenty skeletons from the type locality in the AMNH.
Upper Triassic, Chinle, Petrified Forest Member—North America, New Mexico, Rio Arriba County, Arroyo Seco.

Coelurosaurus Leidy, 1865
Coeluridae, Coelurosauria
[*nomen dubium*]
Genotype: *antiquus.*
Type: Tibia. ANSP 9222.
Upper Cretaceous, Greensand—North America, New Jersey, Burlington County.

Coeluroides Huene and Matley, 1933
Coeluridae, Coelurosauria
[*nomen dubium*]
Genotype: *largus.*
Type: Three dorsal vertebrae. IM K27/562, K27/574, K27/595.
Upper Cretaceous, Lameta Formation—South Asia, India, Jubbulpure.

Coelurus Marsh, 1879
Coeluridae, Coelurosauria
[*nomen dubium*]
Genotype: *fragilis.*
Type: Single dorsal vertebra. YPM 1991.
Upper Jurassic, Morrison Formation—North America, Wyoming, Como Bluff, Quarry 13, Sec. 4, T. 22N, R. 77W.

Compsognathus Wagner, 1859
Coeluridae, Coelurosauria

[valid]
Genotype: *longipes.*
Type: Complete skeleton. IPHG AS1 563.
Upper Jurassic, Kimeridgean, Solnhofen Limestone—Europe, Germany, Bavaria, Solnhofen.

Compsosuchus Huene and Matley, 1933
Coeluridae, Coelurosauria
[*nomen dubium*]
Genotype: *solus.*
Type: Axis. IM K27/578.
Upper Cretaceous, Lameta Formation—South Asia, India, Jubbulpure.

Corythosaurus Brown, 1914
Hadrosauridae, Ornithopoda
[valid]
Genotype: *casuarius.*
Type: Skeleton, lacking forelimbs and end of tail. AMNH 5240.
Upper Cretaceous, Belly River Series, Oldman Formation—North America, Alberta, Steveville.

Craspedodon Dollo, 1883
Iguanodontidae, Ornithopoda
[*nomen dubium*]
Genotype: *lonzeensis.*
Type: Two teeth. IRSNB 390.
Upper Cretaceous, Santonian—Europe, Belgium, Namur, Lonzee.

Crateomus Seeley, 1881
Acanthopholidae, Ankylosauria
[=*Struthiosaurus fide* Romer, 1956]
Genotype: *lepidophorous.*
Type: Jaw, scapula-coracoid, ilium, tibia, ulna, radius, vertebrae, and armor. Geol. Inst. Univ. Vienna.
Upper Cretaceous, Gosau Formation—Europe, Hungary, Siebenbergen.

Craterosaurus Seeley, 1874
Stegosauridae, Stegosauria
[*nomen dubium*]
Genotype: *pottonensis.*
Type: Neural arch of a vertebrae. SM.
Lower Cretaceous, Aptian, Greensand—Europe, England, Potton.

Creosaurus Marsh, 1878
Megalosauridae, Carnosauria
[=*Antrodemus fide* Romer, 1956]
Genotype: *atrox.*
Type: Jugal, premaxilla, two sacral, and one anterior caudal vertebrae, ilium, astragalus, two phalanges, and two claws. YPM 1890.
Upper Jurassic, Morrison Formation—North America, Wyoming, Como Bluff, Quarry I, Sec. 10, T. 22N, R. 77W.

Cryptodraco Lydekker, 1889
Iguanodontidae, Ornithopoda
[provisionally considered valid]
Genotype: *eumerus* Seeley, 1875.
Type: Right femur. SM.
Upper Jurassic, Oxford Clay—Europe, England, Great Gransden.

Cryptosaurus Seeley, 1875
Iguanodontidae, Ornithopoda
[preoccupied=*Cryptodraco fide* Romer, 1956]

Cumnoria Seeley, 1888
Iguanodontidae, Ornithopoda
[=*Camptosaurus fide* Romer, 1956]
Genotype: *prestwichi* Hulke, 1880.
Type: Incomplete skeleton and fragmentary skull. UMO.
Upper Jurassic, Kimeridge Clay—Europe, England, Oxfordshire, Cumnor.
Remarks: This specimen should be thoroughly restudied and carefully compared with *Camptosaurus* so that we can have an up-to-date opinion on whether the two are congeneric.

Cumnovia Carus, 1888
Iguanodontidae, Ornithopoda
[misspelling of *Cumnoria* Seeley, 1888]

Dacentrurus Lucas, 1902
Stegosauridae, Stegosauria
[to replace *Omosaurus* Owen, preoccupied]
Genotype: *armatus* Owen, 1875.
Type: Much of skeleton lacking skull. BMNH 46013.
Upper Jurassic, Kimeridge Clay—Europe, England, Wiltshire, Swindon.

Danubiosaurus Bunzel, 1871
Acanthopholidae, Ankylosauria
[*nomen dubium*]
Genotype: *anceps.*
Type: Fragment of ilium and two rib fragments. Geol. Inst. Univ. Vienna
Upper Cretaceous, Turonian, Gosau Formation—Europe, Hungary, Transylvania, Siebenbergen.

Daspletosaurus D. Russell, 1970
Tyrannosauridae, Carnosauria
[valid]
Genotype: *torosus.*
Type: Skull and skeleton lacking hind limbs. NMC 8506.
Upper Cretaceous, Oldman Formation—North America, Alberta, Steveville.

Dasygnathoides Kuhn, 1961
Ornithosuchidae, Carnosauria
[= *Ornithosuchus fide* Walker, 1964]
Genotype: *longidens* Huxley, 1877.
Type: Impression of part of maxilla with teeth. EM 1R.
Upper Triassic, Elgin Sandstone—Europe, Scotland, Findrasse, near Elgin.

Dasygnathus Huxley, 1877
Ornithosuchidae, Carnosauria
[= *Ornithosuchus fide* Walker, 1964]
Genotype: *longidens.*
Type: Impression of part of maxilla with teeth. EM 1R.
Upper Triassic, Elgin Sandstone—Europe, Scotland, Findrasse, near Elgin.

Deinocheirus Osmolska and Roniewicz, 1967
Dromaeosauridae, Carnosauria
[valid]
Genotype: *mirificus.*
Type: Right and left forelegs and shoulder girdles. Polish Acad. Sci., Warsaw, MGD-1/6.
Upper Cretaceous—East Asia, Mongolia, Gobi Desert.

Deinodon Leidy, 1856
Tyrannosauridae, Carnosauria
[*nomen dubium*]
Genotype: *horridus.*
Type: Twelve isolated and fragmentary teeth. ANSP.
Upper Cretaceous, Judith River Beds—North America, Montana, Chouteau County, Fort Benton, Missouri River.

Deinonychus Ostrom, 1969
Dromaeosauridae, Carnosauria
[valid]
Genotype: *antirrhopus.*
Type: Complete left pes and incomplete right pes. YPM 5205.
Lower Cretaceous, Cloverly Formation—North America, Montana, Carbon County, Sec. 17, T. 7S, R. 24E.

Diceratops Lull, 1905
Ceratopsidae, Ceratopsia
[= *Triceratops fide* Lull, 1933]
Genotype: *hatcheri*
Type: Skull without lower jaws. USNM 2412.
Upper Cretaceous, Lance Formation—North America, Wyoming, Converse County.

Diclonius Cope, 1876
Hadrosauridae, Ornithopoda
[*nomen dubium*]
Genotype: *pentagonus.*
Type: Teeth that have been lost.
Upper Cretaceous, Judith River Formation—North America, Montana, Fergus County, 4 mi. E. of Judith River.

Dicraeosaurus Janensch, 1914
Diplodocidae, Sauropoda
[valid]
Genotype: *hansemanni.*
Type: Vertebrae from second cervical to nineteenth caudal, pelvis, and hind limbs. Humboldt Mus., E. Berlin.
Upper Jurassic, Tendaguru Formation—East Africa, Tanzania, Tendaguru, Kindope.

Didanodon Osborn, 1902
Hadrosauridae, Ornithopoda
[= *Procheneosaurus fide* Lull and Wright, 1942]
Genotype: *altidens* Lambe, 1902.
Type: Left maxilla with teeth. GSC 1092.
Upper Cretaceous, Belly River Series—North America, Alberta, Red Deer River.

Dilophosaurus Welles, 1970
Megalosauridae, Carnosauria
[valid]
Genotype: *wetherilli* Welles, 1954.
Type: Nearly complete skeleton of a juvenile. UCMP 37302.
Lower Jurassic, Kayenta Formation, lower beds—North America, Arizona, Coconino County, near Tuba City.

Dimodosaurus Pidancet and Chopard, 1863
Plateosauridae, Prosauropoda
[= *Plateosaurus fide* Huene, 1907]

Genotype: *poligniensis.*
Type: Remains of five individuals. Museum de Poligny.
Upper Triassic, Rhaetic, lower half of *contorta-zone*—Europe, France, Jura, Poligny.

Dinodocus Owen, 1884
Cetiosauridae, Sauropoda
[*nomen dubium*]
Genotype: *mackesoni.*
Type: Series of broken limb and pelvic bones. BMNH 14695.
Lower Cretaceous, Aptian, Lower Greensand—Europe, England, Kent, Hythe.

Dinodon Cope, 1866
Tyrannosauridae, Carnosauria
[misspelling of *Deinodon* Leidy]

Dinosaurus Rutimeyer, 1856
Teratosauridae, Carnosauria
[=*Gresslyosaurus fide* Romer, 1956]
Genotype: *gresslyi.*
Type: Three sacral and four caudal vertebrae, proximal end of tibia, metacarpal, distal end of metatarsal, claw. Naturhistorisches Museum, Basel.
Upper Triassic, Keuper, Knollenmergel—Europe, Switzerland, Liestal bei Basel.

Diplodocus Marsh, 1878
Diplodocidae, Sauropoda
[valid]
Genotype: *longus.*
Type: Several midcaudal vertebrae. YPM 1920. Supplemented by a skull and most of skeleton collected from same locality.
Upper Jurassic, Morrison Formation—North America, Colorado, Fremont County, Canyon City, Garden Park, Sec. 28, T. 17S, R. 70W.

Diracodon Marsh, 1881
Stegosauridae, Stegosauria
[=*Stegosaurus fide* Romer, 1956]
Genotype: *laticeps.*
Type: Two imperfect maxillae. YPM 1885.
Upper Jurassic, Morrison Formation—North America, Wyoming, Como Bluff, Quarry 13, Sec. 4, T. 22N, R. 77W.

Dolichosuchus Huene, 1932
Podokosauridae, Coelurosauria
[*nomen dubium*]
Genotype: *cristatus.*
Type: Left tibia. BMNH 38058.
Upper Triassic, Upper Keuper, Stubensandstein—Europe, Germany, Wuertemberg.

Doryphorosaurus Nopcsa, 1916
Stegosauridae, Stegosauria
[proposed for *Kentrosaurus* which was thought to be preoccupied.=*nomen nudum*]

Dromaeosaurus Matthew and Brown, 1922
Dromaeosauridae, Carnosauria
[valid]
Genotype: *albertensis.*
Type: Partial skull with lower jaws, hyoids and associated footbones. AMNH 5356.
Upper Cretaceous, Belly River Series, Oldman Formation—North America, Alberta, Red Deer River, Steveville.

Dromiceiomimus Russell, 1972
Ornithomimidae, Coelurosauria
[valid]
Genotype: *brevitertius* Parks, 1926.
Type: Sacrum and adjacent caud. vertebrae, several distal caudals, pelvis, both hind legs; ROM 797.
Upper Cretaceous, late Campanian, Edmonton Formation, member A—North America, southern Alberta, Red Deer River.

Dromicosaurus Hoepen, 1920
Thecodontosauridae, Prosauropoda
[valid]
Genotype: *gracilis.*
Type: Pubes, ischia, femur, tibia, fibula, foot bones, fragments of humerus and radius, a cervical vertebra, and a few caudal vertebrae. TrM.
Upper Triassic, Stormberg Series, Red Beds—South Africa, Orange Free State, Bethlehem.

Dryosaurus Marsh, 1894
Iguanodontidae, Ornithopoda
[valid]
Genotype: *altus* Marsh, 1878.

Type: Tooth, pelvis, and hind leg. YPM 1876.
Upper Jurassic, Morrison Formation—North America, Wyoming, Como Bluff, Quarry 5, Sec. 17, T. 22N, R. 77W.

Dryptosauroides Huene and Matley, 1933
Megalosauridae, Carnosauria
[*nomen dubium*]
Genotype: *grandis.*
Type: Six dorsal vertebrae. IM K20/334, K20/609, K27/549, K27/601, K27/626, K27/602.
Upper Cretaceous, Lameta Formation—South Asia, India, Jubbulpure.

Dryptosaurus Marsh, 1877
Tyrannosauridae, Carnosauria
[valid]
Genotype: *aquilunguis* Cope, 1866.
Type: Portions of jaws, teeth, and skeleton, dorsal and caudal vertebrae, two tibias, astragalus, metatarsals and phalanges. ANSP 9995.
Upper Cretaceous, Greensand—North America, New Jersey, Gloucester County, Barsborough.

Dynamosaurus Osborn, 1905
Tyrannosauridae, Carnosauria
[=*Tyrannosaurus fide* Osborn, 1906]
Genotype: *imperiosus.*
Type: Lower jaws and parts of the skeleton. AMNH 5866.
Upper Cretaceous, Lance Formation—North America, Wyoming, Weston County.

Dyoplosaurus Parks, 1924
Nodosauridae, Ankylosaurus
[valid]
Genotype: *acutisquameus.*
Type: Fragmentary skull and posterior part of axillary skeleton. ROM 784.
Upper Cretaceous, Belly River Series, Oldman Formation—North America, Alberta, Steveville.

Dysalatosaurus Pompeckj, 1920
Iguanodontidae, Ornithopoda
[valid]
Genotype: *lettow-vorbecki.*
Type: Skeleton. Humboldt Museum, E. Berlin.
Upper Jurassic, Kimeridgean, Tendaguru Formation—East Africa, Tanzania, Tendaguru, Kindope.

Dysganus Cope, 1876
Ceratopsidae, Ceratopsia
[*nomen dubium*]
Genotype: *encaustus.*
Type: A single tooth. AMNH 5739.
Upper Cretaceous, Judith River Formation—North America, Montana, Fergus County, Judith River, Dog Creek.

Dystrophaeus Cope, 1877
Camarasauridae, Sauropoda
[*nomen dubium*]
Genotype: *viaemalae.*
Type: Radius, ulna, metacarpals, part of pubis. USNM 2364.
Upper Jurassic, Morrison Formation—North America, Utah, Wayne County, Painted Canyon, Lat. 38° 15′ N. Long. 110° W.

Echinodon Owen, 1861
Stegosauridae, Stegosauria
[=*Saurechinodon fide* Romer, 1956]
Genotype: *becklesi.*
Type: Two fragments of maxillae and two imperfect dentaries. BMNH 48209-12.
Upper Jurassic, Purbeckian—Europe, England, Isle of Purbeck.

Edmontonia Sternberg, 1928
Nodosauridae, Ankylosauria
[valid]
Genotype: *longiceps.*
Type: Skull, right jaw, vertebral column, pelvis, forelimb, hindlimb. NMC 8531.
Upper Cretaceous, Edmonton Formation, Member A—North America, Alberta, Red Deer River, Morrin.

Edmontosaurus Lambe, 1917
Hadrosauridae, Ornithopoda
[valid]
Genotype: *regalis.*
Type: Skull and jaws, vertebrae to 6th caudal, hind limb, humerus, two pubes, one ischium, right ilium. NMC 2288.
Upper Cretaceous, Edmonton Formation, Member A—North America, Alberta, Red Deer River, Three Hills Creek.

Elaphrosaurus Janensch, 1920
Coeluridae, Coelurosauria
[valid]
Genotype: *bambergi.*
Type: Numerous skeletal elements and associated teeth. Humboldt Museum, E. Berlin.
Upper Jurassic, Tendaguru Formation—East Africa, Tanzania, Tendaguru.

Elosaurus Peterson and Gilmore, 1902.
Camarasauridae, Sauropoda.
[*nomen dubium* (a very young animal)]
Genotype: *parvus.*
Type: Scapula, two humeri, ulna, femur, tibia, distal end of right pubis. CM 566.
Upper Jurassic, Morrison Formation—North America, Wyoming, Albany County, Freezeout Hills.

Embasaurus Riabinin, 1931
Megalosauridae, Carnosauria
[*nomen dubium*]
Genotype: *minax.*
Type: Two vertebrae.
Lower Cretaceous, Neocomian Sands—West Asia, Transcaspian Steppes, Mt. Koi-Kara.

Eoceratops Lambe, 1915
Ceratopsidae, Ceratopsia
[valid]
Genotype: *canadensis.*
Type: Right half of skull and right lower jaw. GSC 1254.
Upper Cretaceous, Belly River Series—North America, Alberta, Red Deer River, Steveville.

Empaterius Cope, 1878
Megalosauridae, Carnosauria
[*nomen dubium*]
Genotype: *amplexus.*
Type: Axis, two dorsal vertebrae, coracoid, and fragmentary limb bones. AMNH 5767.
Upper Jurassic, Morrison Formation—North America, Colorado, Fremont County, Canyon City, Garden Park.

Erectopus Huene, 1923
Megalosauridae, Carnosauria
[provisionally considered valid]
Genotype: *superbus* Sauvage, 1882.
Type: Femur, tibia, metatarsals.
Lower Cretaceous, Albian—Europe, North France, Ardennes, Bois de la Panthiere.

Eucamerotus Hulke, 1872
Cetiosauridae, Sauropoda
[*nomen dubium*]
Genotype: No specific name proposed.
Type: Vertebral neural arch. SM.
Lower Cretaceous, Wealden—Europe, England, Isle of Wight.

Eucercosaurus Seeley, 1879
Iguanodontidae, Ornithopoda
[*nomen dubium*]
Genotype: *tanyspondylus.*
Type: A few vertebrae. SM.
Lower Cretaceous, Cambridge Greensand—Europe, England, Cambridge.

Eucnemesaurus Hoepen, 1920
Melanorosauridae, Prosauropoda
[*nomen dubium*]
Genotype: *fortis.*
Type: Proximal end of femur, tibia, proximal part of pubis, a few dorsal and caudal vertebrae. TrM.
Upper Triassic, Stormberg Series, Red Beds—South Africa, Orange Free State, Slabberts.

Euhelopus Romer, 1956
Camarasauridae, Sauropoda
[to replace *Helopus* Wiman, preoccupied]
Genotype: *zdanskyi* Wiman, 1929.
Type: Two partial skeletons that supplement each other.
Lower Cretaceous, Meng Yin Series, lower part—East Asia, China, Shantung, 40 li NW of Meng-Yin-Hsien.

Euoplocephalus Lambe, 1910
Nodosauridae, Ankylosauria
[valid]
Genotype: *tutus* Lambe, 1902.
Type: Upper part of cranium, transverse series of 5-keeled scutes. NMC 210.
Upper Cretaceous, Belly River Series—North America, Alberta, Steveville.

Euscelosaurus Zittel, 1890
Melanorosauridae, Prosauropoda
[misspelling of *Euskelosaurus* Huxley, 1866]

Euscellosaurus Lydekker, 1890
Melanorosauridae, Prosauropoda
[misspelling of *Euskelosaurus* Huxley, 1866]

Euscelesaurus Lydekker, 1890
Melanorosauridae, Prosauropoda
[misspelling of *Euskelosaurus* Huxley, 1866]

Euskelesaurus Huxley, 1867
Melanorosauridae, Prosauropoda
[misspelling of *Euskelosaurus* Huxley, 1866]

Euskelosaurus Huxley, 1866
Melanorosauridae, Prosauropoda
[provisionally considered valid]
Genotype: *browni.*
Type: Femur, tibia, fibula, pubis and fragmentary vertebrae. BMNH R1625.
Upper Triassic, Stormberg Series, Base of Red Beds—South Africa, Cape Province, Kraai River.

Eustreptospondylus Walker, 1964
Megalosauridae, Carnosauria
[valid]
Genotype: *oxoniensis.*
Type: Skeleton. UMO J13558.
Middle Jurassic, Upper Callovian, Middle Oxford Clay—Europe, England, near Oxford.

Fabrosaurus Ginsburg, 1964
Scelidosauridae, Stegosauria
[valid]
Genotype: *australis.*
Type: Incomplete right lower jaw.
Upper Triassic, Stormberg Series, Red Beds—South Africa, Basutoland.

Fulgurotherium Huene, 1932
Coeluridae, Coelurosauria
[provisionally considered valid]
Genotype: *australe.*
Type: Femur. BMNH 3719.
Lower Cretaceous, Aptian—Australia, New South Wales.

Gallimimus Osmolska, Roniewicz & Barsbold, 1972
Ornithomimidae, Coelurosauria
[valid]
Genotype: *bullatus.*
Type: Complete skeleton. Geol. Inst. Acad. Sci., Mongolian People's Republic, DPS 100/11.
Upper Cretaceous, Maestrichtian, upper Nemegt beds—East Asia, Mongolia, Gobi Desert, Nemegt Basin.

Genyodectes Woodward, 1901
Tyrannosauridae, Carnosauria
[valid]
Genotype: *serus.*
Type: Partial skull with lower jaws. MLP.
Upper Cretaceous, Upper Senonian—South America, Argentina, Chubut, Cañadon Grande.

Geranosaurus Broom, 1911
Hypsilophodontidae, Ornithopoda
[valid]
Genotype: *atavus.*
Type: Fragmentary skull, lower jaws, tibia, fibula, and partial foot. SAFM 1871.
Upper Triassic, Stormberg Series, Base of Cave Sandstone—South Africa, Cape Province, Barkley Pass.

Gigantosaurus Fraas (non Seeley), 1908
Diplodocidae, Sauropoda
[= *Tornieria* Sternfeld, 1911]
Genotype: *robusta* Fraas, 1908.
Type: Second caudal and a midcaudal vertebrae, right ischium, right femur, and right tibia.
Upper Jurassic, Kimeridgean, Tendaguru Formation—East Africa, Tanzania, Tendaguru.

Gigantosaurus Seeley (non Fraas), 1869
Cetiosauridae, Sauropoda
[*nomen dubium*]
Genotype: *megalonyx.*
Type: Fibula and terminal phalanx. BMNH 32498-99.
Upper Jurassic, Kimeridgean, Kimeridge Clay—Europe, England, Cambridgeshire, Ely.

Gigantoscelus Hoepen, 1916
Melanorosauridae, Prosauropoda
[*nomen dubium*]
Genotype: *molengraaffi.*
Type: Distal end of femur. TrM.
Upper Triassic, Stormberg Series, Bushveld Sandstone—South Africa, Transvaal, Haakdoornbult.

Gorgosaurus Lambe, 1914
Tyrannosauridae, Carnosauria
[=*Albertosaurus fide* D. Russell, 1970]
Genotype: *libratus.*
Type: Nearly entire skeleton. NMC 2120.
Upper Cretaceous, Oldman Formation —North America, Alberta, near Steveville.

Gresslyosaurus Rütimeyer, 1857
Teratosauridae, Carnosauria
[*nomen dubium*]
Genotype: *ingens.*
Type: Sacrum, four caudal vertebrae, proximal end of tibia, partial foot. Naturhistorisches Museum, Basel.
Upper Triassic, Keuper, Knollenmergel —Europe, Switzerland, Basel.

Gryponyx Broom, 1911
Thecodontosauridae, Prosauropoda
[valid]
Genotype: *africanus.*
Type: Pelvis, hind limbs, right and left manus, and vertebrae. SAFM 3357, 3358, 3359.
Upper Triassic, Stormberg Series, top of Red Beds—South Africa, Orange Free State, Fouriesburg.

Gryposaurus Lambe, 1914
Hadrosauridae, Ornithopoda
[=*Kritosaurus* Brown, 1910]
Genotype: *notabilis.*
Type: Skull, jaws, vertebrae, pectoral girdle, pelvis, one hind leg. NMC 2278.
Upper Cretaceous, Belly River Series, Oldman Formation—North America, Alberta, Belly River.

Gyposaurus Broom, 1911
Thecodontosauridae, Prosauropoda
[valid]
Genotype: *capensis.*
Type: Partial skeleton in a slab of sandstone. SAFM 990.
Upper Triassic, Stormberg Series, Cave Sandstone—South Africa, Orange Free State, Ladybrand.

Gwyneddosaurus Bock, 1945
[uncertain position—has been referred to the Coelurosauria and Protosauria]
Genotype: *erici.*
Type: Poorly preserved skeleton. ANSP 15072.
Upper Triassic, Lockatong Formation—North America, Pennsylvania.

Hadrosaurus Leidy, 1858
Hadrosauridae, Ornithopoda
[valid]
Genotype: *foulkii.*
Type: Mandibular teeth, 28 vertebrae, humerus, radius, ulna, ilium, ischium, femur, tibia, fibula and two metatarsals. ANSP 10005.
Upper Cretaceous, Monmouth, Woodbury Formation—North America, New Jersey, Haddonfield.

Hallopus Marsh, 1881
Hallopodidae, Coelurosauria
[removed to Crocodilia, Walker, 1970]

Halticosaurus Huene, 1908
Procompsognathidae, Coelurosauria
[valid]
Genotype: *longotarsus.*
Type: Fragmentary skeleton. SMNS.
Upper Triassic, Stubensandstein—Europe, Germany, Halberstadt.

Haplocanthus Hatcher, 1903
Cetiosauridae, Sauropoda
[preoccupied=*Haplocanthosaurus* Hatcher, 1903]

Haplocanthosaurus Hatcher, 1903
Cetiosauridae, Sauropoda
[valid]
Genotype: *priscus.*
Type: Dorsal, sacral and caudal vertebrae, pelvis, scapula-coracoid, femur. CM 572.
Upper Jurassic, Morrison Formation—North America, Colorado, Fremont County, Canyon City, Garden Park, Sec. 28, T. 17S, R. 70W.

Hecatosaurus Brown, 1910
Hadrosauridae, Ornithopoda
[=*Telmatosaurus* Nopcsa, 1903]
Genotype: *transylvanicus* Nopcsa, 1900.
Type: Skull.
Upper Cretaceous, Turonian, Gosau Formation—Europe, Hungary, Transylvania.

Heishansaurus Bohlin, 1953
Nodosauridae, Ankylosauria
[valid]
Genotype: *pachycephalus.*
Type: Skull, skeleton and dermal armor.

Upper Cretaceous, Djadocta equivalent—East Asia, China, West Kansu, Chia-Yu-Kuan.

Helopus Wiman, 1929
Camarasauridae, Sauropoda
[preoccupied = *Euhelopus* Romer, 1956]
Genotype: *zdanskyi.*
Type: Two partial skeletons that supplement each other.
Lower Cretaceous, Meng Yin Series, lower part—East Asia, China, Shantung, Meng Yin.

Herrerasaurus Reig, 1963
Plateosauridae, Prosauropoda
[valid]
Genotype: *ischigualastensis.*
Type: Incomplete remains of 5 individuals.
Middle Triassic, Ladinian, Ischigualasto Formation—South America, Argentina, San Juan and La Rioja.

Heterodontosaurus Crompton and Charig, 1962
Hypsilophodontidae, Ornithopoda
[valid]
Genotype: *tucki.*
Type: Nearly complete skull, lower jaw and partial skeleton. SAFM K337.
Upper Triassic, Stormberg Series, Cave Sandstone—South Africa, Cape Province, Herschel district.

Hierosaurus Wieland, 1909
Nodosauridae, Ankylosauria
[provisionally considered valid]
Genotype: *sternbergii.*
Type: Nearly 70 dermal elements. YPM 1847.
Upper Cretaceous, Niobrara Formation—North America, Kansas, Logan County.

Hoplitosaurus Lucas, 1902
Nodosauridae, Ankylosauria
[*nomen dubium fide* Ostrom, 1970]
Genotype: *marshi* Lucas, 1901.
Type: Right femur, proximal half of left humerus, distal half of right humerus, right scapula-coracoid, numerous dermal plates. USNM 4752.
Lower Cretaceous, Lakota Formation—North America, South Dakota, Custer County, Buffalo Gap, Calico Canyon.

Hoplosaurus Lydekker, 1890
Cetiosauridae, Sauropoda
[*nomen dubium*]
Genotype: *armatus* Gervais, 1852.
Type: A single tooth. BMNH R964.
Lower Cretaceous, Wealden—Europe, England, Isle of Wight.

Hortalotarsus Seeley, 1894
Thecodontosauridae, Prosauropoda
[*nomen dubium*]
Genotype: *skirtopodus.*
Type: Fragment of a hind limb. Albany Museum, South Africa.
Upper Triassic, Stormberg Series, Cave Sandstone—South Africa, Cape Province, Barkley East.

Hylaeosaurus Mantell, 1833
Acanthopholidae, Ankylosauria
[valid]
Genotype: *oweni.*
Type: Base of skull, 10 anterior vertebrae, two coracoids, two distal parts of scapulae, loose vertebrae, several ribs and dermal spines. BMNH 3775.
Lower Cretaceous, Wealden—Europe, England, Sussex, Tilgate Forest.

Hylosaurus Fitzinger, 1843
Acanthopholidae, Ankylosauria
[misspelling of *Hylaeosaurus* Mantell, 1833]

Hypacrosaurus Brown, 1913
Hadrosauridae, Ornithopoda
[valid]
Genotype: *altispinus.*
Type: Last eight dorsal and two anterior caudal vertebrae, two ilia, right ischium, right pubis, several ribs. AMNH 5204.
Upper Cretaceous, Edmonton Formation, Member B—North America, Alberta, Tolman Ferry.

Hypselorhachis Charig (in Harland et al), 1967
Spinosauridae, l.s., Carnosauria
[*nomen nudum*]
Genotype: *mirabilis.*
Type: Single vertebra with very long neural spine.
Middle Triassic, Anisian, Manda Formation—East Africa, Tanzania, Ruhuhu Basin.

Hypselosaurus Matheron, 1869
Diplodocidae, Sauropoda
[provisionally considered valid]
Genotype: *priscus.*
Type: Femur. MNHN.
Upper Cretaceous, Maestrichtian—Europe, France, Provence, Rognac.

Hypsibema Cope, 1870
Hadrosauridae, Ornithopoda
[*nomen dubium fide* Lull and Wright, 1942]
Genotype: *crassicauda.*
Type: Caudal centrum, distal end of humerus, tibial shaft, and a metatarsal. USNM 7189.
Upper Cretaceous, Black Creek Formation—North America, North Carolina, Sampson County.

Hypsilophodon Huxley, 1870
Hypsilophodontidae, Ornithopoda
[valid]
Genotype: *foxi.*
Type: Imperfect skull and mandible. BMNH R197.
Lower Cretaceous, Wealden—Europe, England, Isle of Wight, Cowleaze Chine.

Hypsirophus Cope, 1878
Stegosauridae, Stegosauria
[*nomen dubium*]
Genotype: *discursus.*
Type: A number of dorsal and caudal vertebrae. AMNH 5731.
Upper Jurassic, Morrison Formation—North America, Colorado, Fremont County, Canyon City, Garden Park.

Iguanodon Mantell, 1825
Iguanodontidae, Ornithopoda
[valid]
Genotype: *anglicum* Holl, 1829.
Type: Teeth. BMNH 2392.
Lower Cretaceous, Wealden—Europe, England, Kent.

Iguanosaurus Ritgen, 1828
Iguanodontidae, Ornithopoda
[= *Iguanodon fide* Romer, 1956]

Iliosuchus Huene, 1932
Megalosauridae, Carnosauria
[= *Megalosaurus fide* Romer, 1956]
Genotype: *incognitus.*
Type: Ilium. BMNH R83.
Middle Jurassic, Bathonian, Great Oolite—Europe, England, Stonesfield.

Indosaurus Huene and Matley, 1933
Megalosauridae, Carnosauria
[provisionally considered valid]
Genotype: *matleyi.*
Type: Braincase including most of frontals. IM K27/565.
Upper Cretaceous, Lameta Formation—South Asia, India, Jubbulpure.

Indosuchus Huene and Matley 1933
Tyrannosauridae, Carnosauria
[provisionally considered valid]
Genotype: *raptorius.*
Type: Frontal region of skull consisting of frontals, parts of prefrontals, and parts of parietals. IM K20/350.
Upper Cretaceous, Lameta Formation—South Asia, India, Jubbulpure, Bara Simla Hill.

Inosaurus Lapparant, 1960
Megalosauridae, Carnosauria
[*nomen dubium*]
Genotype: *tedreftensis.*
Type: One caudo-sacral, one anterior caudal, and one midcaudal, vertebra.
Lower Cretaceous, Continental Intercalaire—Africa, Sahara Central, Niger, In Abangarit.

Ischisaurus Reig, 1963
Plateosauridae, Prosauropoda
[valid]
Genotype: *cattoi.*
Type: Skull fragments, parts of maxillae, premaxillae, lower jaws, limb and girdle elements, and vertebrae.
Middle Triassic, Ischigualasto Formation—South America, Argentina, San Juan province.

Ischyrosaurus Hulke, 1874
Cetiosauridae, Sauropoda
[*nomen dubium*]
Genotype: *manseli.*
Type: Left humerus, lacking deltoid crest. BMNH 41626.
Upper Jurassic, Kimeridge Clay—Europe, England, Dorsetshire, Kimeridge Bay.

Jaxartosaurus Riabinin, 1939
Hadrosauridae, Ornithopoda
[valid]
Genotype: *aralensis.*
Type: Posterior part of skull, several

vertebrae, and limb bones.
PEN AN SSR 1/5009.
Upper Cretaceous, Cenomanian-Turonian—Central Asia, Kazakstan, Sary-Agach RR Station.

Jubbulpuria Huene and Matley, 1933
Coeluridae, Coelurosauria
[*nomen dubium*]
Genotype: *tenuis*.
Type: Two dorsal vertebrae. IM K27/614, K20/612.
Upper Cretaceous, Lameta Formation—South Asia, India, Jubbulpure, Bara Simla Hill.

Kangnasaurus Haughton, 1915
Iguanodontidae, Ornithopoda
[*nomen dubium*]
Genotype: *coetzeei*.
Type: Tooth. SAFM 2732.
Cretaceous—South Africa, Bushmanland, Farm Kangnas.

Kentrosaurus Hennig, 1915
Stegosauridae, Stegosauria
[valid]
Genotype: *aethiopicus*.
Type: Nearly entire skeleton.
Upper Jurassic, Tendaguru Formation—East Africa, Tanzania, Kindope.

Kentrurosaurus Hennig, 1917
Stegosauridae, Stegosauria
[=*Kentrosaurus fide* Romer, 1956]

Kladeistereodon Pleininger, 1846
Teratosauridae, Carnosauria
[misspelling of *Cladeiodon* Owen, 1841]

Kladyodon Pleininger, 1846
Teratosauridae, Carnosauria
[misspelling of *Cladeiodon* Owen, 1841]

Kritosaurus Brown, 1910
Hadrosauridae, Ornithopoda
[valid]
Genotype: *navajovius*.
Type: Skull lacking rostrum and lower jaws. AMNH 5799.
Upper Cretaceous, Kirtland Formation—North America, New Mexico, San Juan County, near Ojo Alamo.

Labrosaurus Marsh, 1879
Megalosauridae, Carnosauria
[=*Antrodemus fide* Romer, 1956]
Genotype: *lucaris* Marsh, 1878.
Type: Several cervical, six dorsal and two sacral vertebrae, two humeri, parts of radius and ulna, scapula-coracoid, one phalanx. YPM 1931.
Upper Jurassic, Morrison Formation—North America, Wyoming, Como Bluff, Quarry 3, Sec. 11, T. 22N, R. 77W.

Laelaps Cope, 1866
Tyrannosauridae, Carnosauria
[preoccupied=*Dryptosaurus* Marsh, 1877]
Genotype: *aguilunguis*.
Type: Portions of jaws with teeth, dorsal and caudal vertebrae, two tibias, astragalus, metatarsals and phalanges. ANSP.
Upper Cretaceous, Greensand—North America, New Jersey, Gloucester County, Barsborough.

Laevisuchus Huene and Matley, 1933
Coeluridae, Coelurosauria
[*nomen dubium*]
Genotype: *indicus*.
Type: Three cervical vertebrae. IM K20/613, K20/614, K27/696.
Upper Cretaceous, Lameta Formation—South Asia, India, Jubbulpure, Bara Simla Hill.

Lambeosaurus Parks, 1923
Hadrosauridae, Ornithopoda
[valid]
Genotype: *lambei*.
Type: Skull and right lower jaw. GSC 1218.
Upper Cretaceous, Belly River Series—North America, Alberta, Red Deer River, Little Sandhill Creek.

Lametasaurus Matley, 1923
Nodosauridae, Ankylosauria
[provisionally considered valid]
Genotype: *indicus*.
Type: About 5000 scutes of *Hoplitosaurus*-type (fide Walker, 1964). IM.
Upper Cretaceous, Lameta Formation—South Asia, India, Jubbulpure.

Laosaurus Marsh, 1878
Hypsilophodontidae, Ornithopoda
[*nomen dubium*]
Genotype: *celer*.
Type: Two complete vertebral centra and nine half centra. YPM 1874.

Upper Jurassic, Morrison Formation—North America, Wyoming, Como Bluff, Quarry 9?

Laplatasaurus Huene, 1928
Diplodocidae, Sauropoda
[valid]
Genotype: *araukanicus.*
Type: Ten caudal vertebrae, scapula-coracoid, sternal plates, humerus, radius, ulna, manus, ilium, tibia. MLP.
Upper Cretaceous, Senonian—South America, Argentina, Neuquén.

Leipsanosaurus Nopcsa, 1918
Acanthopholidae, Ankylosauria
[*nomen dubium*]
Genotype: *noricus.*
Type: A single tooth.
Upper Cretaceous, Turonian, Gosau Formation—Europe, Hungary, Transylvania.

Lepanosaurus Romer et al, 1962
Acanthopholidae, Ankylosauria
[=misspelling of *Leipsanosaurus* Nopcsa, 1918]

Leptoceratops Brown, 1914
Protoceratopsidae, Ceratopsia
[valid]
Genotype: *gracilis.*
Type: Parts of skull and jaws, caudal vertebrae, complete front limb, parts of hind limbs. AMNH 5205.
Upper Cretaceous, Edmonton Formation—North America, Alberta, Tolman Ferry.

Leptospondylus Owen, 1853
Thecodontosauridae, Prosauropoda
[*nomen dubium fide* Broom, 1911]
Genotype: *capensis.*
Type: Imperfect vertebra. RCS. Destroyed.
Upper Triassic, Stormberg Series, Red Beds—South Africa, Harrismith, Beaucherf.

Lexovisaurus Hoffstetter, 1957
Stegosauridae, Stegosauria
[valid]
Genotype: *durobrivensis* Hulke, 1887.
Type: Part of pelvis, vertebral centra, left femur, dermal armor including spikes and plates. BMNH R1989.
Middle Jurassic, Callovian—Europe, England, Peterborough.

Limnosaurus Nopcsa, 1900
Hadrosauridae, Ornithopoda
[preoccupied=*Telmatosaurus* Nopcsa, 1903]
Genotype: *transylvanicus.*
Type: Skull.
Upper Cretaceous, Turonian, Gosau Formation—Europe, Hungary, Transylvania.

Loncosaurus Ameghino, 1899
Coeluridae, Coelurosauria
[provisionally considered valid]
Genotype: *argentinus.*
Type: Femur. MLP.
Upper Cretaceous, Upper Senonian—South America, Argentina, Santa Cruz, Rio Sehuen.

Lophorhothon Langston, 1960
Hadrosauridae, Ornithopoda
[valid]
Genotype: *alopus.*
Type: Partial skeleton with skull. FM P27383.
Upper Cretaceous, Campanian, Selma Chalk—North America, Alabama, Dallas County, 10 mi. W of Selma.

Loricosaurus Huene, 1929
Nodosauridae, Ankylosauria
[provisionally considered valid]
Genotype: *scutatus.*
Type: Twenty-six dermal ossifications. MLP.
Upper Cretaceous, Upper Senonian—South America, Argentina, Rio Negro, Cinco Saltos.

Lufengosaurus Young, 1941
Plateosauridae, Prosauropoda
[valid]
Genotype: *huenei.*
Type: Nearly entire skeleton. GSC V15 LVP.
Upper Triassic, Lufeng Series, Purplish Beds—East Asia, China, Yunnan, Lufeng.

Lukousaurus Young, 1948
Procompsognathidae, Coelurosauria
[valid]
Genotype: *yini.*
Type: Anterior part of skull and jaws. IVP AS V23.
Upper Triassic, Lower Lufeng Series, Dark Red Beds—East Asia, China, Yunnan, Lufeng, Huangchiatien.

Lusitanosaurus Lapparent and Zbyszewski, 1957
Scelidosauridae, Stegosauria
[valid]
Genotype: *liasicus.*
Type: Left maxilla. Univ. Lisbon.
Lower Jurassic, Lias, Sinemurian—Europe, Portugal, Saõ Pedro de Muel.

Lycorhinus Haughton, 1924
Heterodontosauridae, Ornithopoda
[valid]
Genotype: *angustidens.*
Type: Portion of left lower jaw with seven teeth. SAFM 3606 (lost).
Upper Triassic, Stormberg Series, Red Beds—South Africa, Cape Province, Paballong, Mt. Fletcher.

Macelognathus Marsh, 1884
referred to Crocodilia, Ostrom 1971
[provisionally considered valid]
Genotype: *vagans.*
Type: Symphyseal and anterior portions of left and right dentaries. YPM 1415.
Upper Jurassic, Morrison Formation—North America, Wyoming, Como Bluff, Quarry 9, SW¼, Sec. 12, T. 22N, R. 77W.

Macrodontophion Zborzewski, 1834
Megalosauridae, Carnosauria
[*nomen dubium*]
Genotype: No specific designation.
Type: Tooth.
Jurassic—Europe, U.S.S.R., Podolie-Volhyniennes.

Macrophalangia Sternberg, 1932
Ornithomimidae, Coelurosauria
[valid]
Genotype: *canadensis.*
Type: Right foot with first digit. NMC 8538.
Upper Cretaceous, Belly River Series, Oldman Formation—North America, Alberta, Red Deer River.

Macrurosaurus Seeley, 1869
Diplodocidae, Sauropoda
[provisionally considered valid]
Genotype: *semnus.*
Type: Forty caudal vertebra. SM.
Lower Cretaceous, Upper Greensand—Europe, England, Cambridge.

Maggiarosaurus Huene, 1956
Diplodocidae, Sauropoda
[misspelling of *Magyarosaurus* Huene, 1932]

Magnosaurus Huene, 1932
Megalosauridae, Carnosauria
[=*Megalosaurus fide* Romer, 1956]
Genotype: *nethercombensis.*
Type: Jaws with teeth, a dorsal vertebra, two tibia, and part of right pubis. UMO.
Middle Jurassic, inferior oolite, hunphriesei Zone—Europe, England, Dorsetshire.

Magyarosaurus Huene, 1932
Diplodocidae, Sauropoda
[*nomen dubium*]
Genotype: *dacus.*
Type: Dorsal centrum, caudal vertebrae, right humerus, right ulna, left fibula. BMNH R3861a.
Upper Cretaceous, Turonian, Gosau Formation—Europe, Hungary, Siebenbergen.

Majungasaurus Lavocat, 1955
Megalosauridae, Carnosauria
[provisionally considered valid]
Genotype: *crenatissimus* Depéret, 1896.
Type: Incomplete right dentary.
Upper Cretaceous, Berivotro Formation—Madagascar, Berivotro.

Mamenchisaurus Young, 1954
Diplodocidae, Sauropoda
[valid]
Genotype: *constructus.*
Type: Partial skeleton. IVP AS.
Upper Jurassic, Red Beds—East Asia, China, Szechuan, Yiping, Mamenchi.

Mandchurosaurus Riabinin, 1930
Hadrosauridae, Ornithopoda
[valid]
Genotype: *amurensis.*
Type: Incomplete skeleton. Mus. Geol. Inst., Leningrad.
Upper Cretaceous, Lance Equivalent—East Asia, Manchuria, Belye Kinchi.

Manospondylus Cope, 1892
Tyrannosauridae, Carnosauria
[*nomen dubium fide* Marsh, Hatcher and Lull, 1907]
Genotype: *gigas.*
Type: Centrum of a dorsal vertebra. AMNH 3982.

Upper Cretaceous, Maestrichian, Lance Formation—North America, South Dakota.

Marcellognathus Romer, 1966
Hypsilophodontidae, Ornithopoda
[misspelling of *Macelognathus* Marsh, 1884]

Massospondylus Owen, 1854
Thecodontosauridae, Prosauropoda
[valid]
Genotype: *carinatus.*
Type: Cervical, a few dorsal and a few caudal vertebrae, scapula, humerus, ilium, pubis, femur, tibia. RCS. Destroyed.
Upper Triassic, Stormberg Series, Red Beds—South Africa, Orange Free State, Harrismith.

Megadactylus Hitchcock, 1865
Thecodontosauridae, Prosauropoda
[preoccupied=*Anchisaurus* Marsh, 1885]
Genotype: *polyzelus.*
Type: One dorsal and four caudal vertebrae, right manus, distal ends of radius and ulna, two ischia, left femur, proximal end of tibia, left fibula, and pes. AC 41/109-118.
Upper Triassic, Newark Series, Longmeadow Sandstone—North America, Massachusetts, Hampden County, Springfield.

Megalosaurus Buckland, 1824
Megalosauridae, Carnosauria
[valid]
Genotype: *bucklandi* von Meyer, 1832.
Type: Right dentary with teeth. UMO J13506.
Middle Jurassic, Middle Bathonian, Stonesfield Slates—Europe, England, Oxford, Woodstock.

Melanorosaurus Haughton, 1924
Melanorosauridae, Prosauropoda
[valid]
Genotype: *readi.*
Type: Femur, tibia, fibula, proximal end of humerus, and some vertebrae. SAFM 3449, 3450.
Upper Triassic, Stormberg Series, Red Beds—South Africa, Cape Province, Herschel.

Metricanthosaurus Walker, 1964
Megalosauridae, Carnosauria
[valid]
Genotype: *parkeri* Huene, 1926.
Type: Pelvis, right femur, and vertebral column. UMO 12144.
Upper Jurassic, Lower Oxfordian, Oxford Clay—Europe, England, Dorset, 1½ mi. N of Weymouth.

Microceratops Bohlin, 1953
Protoceratopsidae, Ceratopsia
[valid]
Genotype: *gobiensis.*
Type: Fragmentary dentary.
Upper Cretaceous, Djadocta equivalent—East Asia, Western Kansu, Tsondolein-Khuduk.

Microcoelus Lydekker, 1894
Diplodocidae, Sauropoda
[*nomen dubium*]
Genotype: *patagonicus.*
Type: Anterior dorsal and caudal vertebrae, humerus.
Upper Cretaceous, Senonian—South America, Argentina, Neuquen.

Microsaurops Kuhn, 1964
Diplodocidae, Sauropoda
[to replace *Microsaurus* Hatcher, 1900]

Microsaurus Hatcher, 1900
Diplodocidae, Sauropoda
[preoccupied=*Microsaurops* Kuhn, 1964]
Genotype: Information not available.
Type: Information not available.
Upper Cretaceous, Guaranitic Beds—South America, Argentina.

Microvenator Ostrom, 1970
Coeluridae, Coelurosauria
[valid]
Genotype: *celer.*
Type: Partial skeleton lacking skull. AMNH 3041.
Lower Cretaceous, Cloverly Formation, Unit VII—North America, Montana, Wheatland County, SW¼, Sec. 26, T. 7N, R. 16E.

Mochlodon Seeley, 1881
Iguanodontidae, Ornithopoda
[=*Rhabdodon fide* Romer, 1956]

Mongolosaurus Gilmore, 1933
Diplodocidae, Sauropoda

[*nomen dubium*]
Genotype: *haplodon.*
Type: Fragmentary teeth, basioccipital, atlas, axis and third cervical vertebra. AMNH 6710.
Lower Cretaceous, OnGong Formation—East Asia, Mongolia, Hu Khung Ulan.

Monoclonius Cope, 1876
Ceratopsidae, Ceratopsia
[valid]
Genotype: *crassus.*
Type: Fused parietals, sacrum and anterior dorsal vertebrae. AMNH 3998.
Upper Cretaceous, Judith River Formation—North America, Montana, N side of Missouri River between Chouteau and Blaine Counties.

Montanaceratops Sternberg, 1951
Protoceratopsidae, Ceratopsia
[valid]
Genotype: *cerorhynchus* Brown and Schlaikjer, 1942.
Type: Parts of skull and jaws and most of postcranial skeleton. AMNH 5464.
Upper Cretaceous, St. Mary's River Formation (Lance)—North America, Montana, Glacier County, Blackfeet Indian Res.

Morinosaurus Sauvage, 1874
Camarasauridae, Sauropoda
[*nomen dubium fide* Janensch, 1935]
Genotype: *typus.*
Type: A greatly worn tooth.
Upper Jurassic, Upper Kimeridgean—Europe, France, Boulogne-sur-Mer.

Morosaurus Marsh, 1878
Camarasauridae, Sauropoda
[=*Camarasaurus fide* Mook, 1914]
Genotype: *impar=grandis.*
Type: Sacrum. YPM 1900.
Upper Jurassic, Morrison Formation—North America, Wyoming, Como Bluff, Quarry 1, Sec. 10, T. 22N, R. 77W.

Nanosaurus Marsh, 1877
Hypsilophodontidae, Ornithopoda
[valid]
Genotype: *agilis.*
Type: Lower jaw, one ilium, two ischia, one pubis, two femora, two tibias, one fibula, one humerus. YPM 1913.
Upper Jurassic, Morrison Formation—North America, Colorado, Fremont County, Canyon City, Garden Park.

Nemegtosaurus Nowinski, 1971
Diplodocidae, Sauropoda
[valid]
Genotype: *mongoliensis.*
Type: Skull, jaws, and much of postcranium excluding cervical column. Paleozoological Inst., Polish Acad. Sciences, Warsaw. MgD-I/9.
Upper Cretaceous, Maestrichtian, upper Nemegt beds—East Asia, Mongolia, Gobi Desert, Nemegt Basin.

Neosaurus Gilmore, 1945
Camarasauridae, Sauropoda
[preoccupied=*Parrasaurus* Gilmore, 1945]
Genotype: *missouriensis.*
Type: Thirteen midcaudal centra. USNM 16735.
Upper Cretaceous, Ripley Formation, McNary sand member—North America, Missouri, Bollinger County, Glen Allen.

Neosodon Moussaye, 1885
Cetiosauridae, Sauropoda
[*nomen dubium*]
Genotype: *praecursor* Sauvage, 1876.
Type: Teeth.
Upper Jurassic, Portlandian—Europe, France, Boulogne.

Nipponosaurus Nagao, 1936
Hadrosauridae, Ornithopoda
[valid]
Genotype: *sachaliensis.*
Type: Posterior part of skull, a few cervical, a few dorsal, sacrum and caudal vertebrae, scapula, ilium, two ischia, two humeri, distal end of femur.
Upper Cretaceous, Upper Senonian—East Asia, Japan, Saghalien, Kawa Kami.

Nodosaurus Marsh, 1889
Nodosauridae, Ankylosauria
[valid]
Genotype: *textilis.*
Type: Several dorsal vertebrae, sacrum, ilium, left hind leg, parts of two humeri, left radius, ulna, manus, scutes. YPM 1815.
Lower Cretaceous, (?) Dakota Forma-

tion—North America, Wyoming, Albany County, 10 to 12 miles E of Como Bluff.

Notoceratops Tapia, 1918
Ceratopsidae, Ceratopsia
[valid]
Genotype: *bonarelli.*
Type: Incomplete left dentary.
Upper Cretaceous, Upper Senonian—South America, Argentina, Chubut, Colhue Huapi.

Nuthetes Owen, 1854
Lacertilia, non Carnosaur

Nyasaurus Charig (in Harland et al.), 1967
Anchisauridae (or adv. Prestosuchidae)
[*nomen nudum*]
Genotype: *cromptoni.*
Type: Material not mentioned. BMNH.
Middle Triassic, Anisian, Manda Formation—East Africa, Tanzania, Ruhuhu Basin.

Omeisaurus Young, 1939
Camarasauridae, Sauropoda
[valid]
Genotype: *junghsiensis.*
Type: Four cervical, three dorsal, 13 sacral and postsacral vertebrae, humerus, two ilia, two ischia, one pubis, proximal end of femur and fibula. IVP AS.
Upper Jurassic—East Asia, China, Szechuan, Junghsien.

Omosaurus Owen, 1875
Stegosauridae, Stegosauria
[preoccupied (Leidy, 1856) = *Dacentrurus* Lucas, 1902]
Genotype: *armatus.*
Type: Much of skeleton lacking skull. BMNH 46013.
Upper Jurassic, Kimeridgean, Kimeridge Clay—Europe, England, Wiltshire, Swindon.

Onychosaurus Nopcsa, 1902
Acanthopholidae, Ankylosauria
[valid]
Genotype: *hungaricus.*
Type: Remains of two individuals.
Upper Cretaceous, Turonian, Gosau Formation—Europe, Hungary, Siebenbergen.

Oplosaurus Gervais, 1852
Cetiosauridae, Sauropoda
[*nomen dubium*]
Genotype: *armatus.*
Type: A single tooth. BMNH R964.
Lower Cretaceous, Wealden—Europe, England, Isle of Wight.

Orinosaurus Lydekker, 1889
Melanorosauridae, Prosauropoda
[*nomen dubium* = *Orosaurus* Huxley, 1867]
Genotype: *capensis.*
Type: Proximal end of left tibia. BMNH 1626.
Upper Triassic, Stormberg Series—South Africa, Aliwal North.

Ornitholestes Osborn, 1903
Coeluridae, Coelurosauria
[valid]
Genotype: *hermani.*
Type: Nearly entire skeleton. AMNH 619.
Upper Jurassic, Morrison Formation—North America, Wyoming, Albany County, near Como, Bone Cabin Quarry.

Ornithomerus Seeley, 1881
Hadrosauridae, Ornithopoda
[*nomen dubium*]
Genotype: *gracilis.*
Type: Shaft of femur. Geol. Mus. Univ. Vienna.
Upper Cretaceous, Turonian, Gosau Formation—Europe, Austria, Wiener-Neustadt.

Ornithomimoides Huene and Matley, 1933
Ornithomimidae, Coelurosauria
[*nomen dubium*]
Genotype: *mobilis.*
Type: Five dorsal vertebrae. IM K20/610, K20/614B, K27/597, K27/600, K27/610.
Upper Cretaceous, Lameta Formation—South Asia, India, Jubbulpure, Bara Simla Hill.

Ornithomimus Marsh, 1890
Ornithomimidae, Coelurosauria
[valid]
Genotype: *velox.*
Type: Distal end of tibia, astragalus, calcaneum, three metatarsals, three

phalanges of 2nd digit. YPM 542.
Upper Cretaceous, Denver Formation—North America, Colorado, Jefferson County, SW¼, Sec. 27, T. 4S, R. 69W.

Ornithopsis Seeley, 1870
Cetiosauridae, Sauropoda
[*nomen dubium*]
Genotype: *hulkei.*
Type: Imperfect centrum of anterior dorsal vertebra. BMNH 28632.
Lower Cretaceous, Wealden—Europe, England, Isle of Wight.

Ornithosuchus Newton, 1894
Ornithosuchidae, Carnosauria
[valid]
Genotype: *woodwardi* Newton, 1894 = *longidens* Huxley, 1877.
Type: Skull, vertebrae from third dorsal to midcaudal, pelvis, and parts of hind limbs. BMNH R2409 and R2410.
Upper Triassic, Elgin Sandstone—Europe, Scotland, Elgin.

Ornithotarsus Cope, 1869
Hadrosauridae, Ornithopoda
[*nomen dubium*]
Genotype: *immanis.*
Type: Distal ends of left tibia and fibula with astragulus and calcaneum. YPM 3221.
Upper Cretaceous, Monmouth Formation—North America, New Jersey, Monmouth County, Union, Raritan Bay.

Orosaurus Huxley, 1867
Melanosauridae, Prosauropoda
[*nomen dubium fide* Huene, 1932]
Genotype: *capensis* Lydekker, 1889.
Type: Proximal end of left tibia. BMNH R1626.
Upper Triassic, Stormberg Series—South Africa, Aliwal North.

Orthogoniosaurus Das-Gupta, 1931
Coeluridae, Coelurosauria
[*nomen dubium*]
Genotype: *matleyi.*
Type: A single tooth. IM.
Upper Cretaceous, Lameta Formation—South Asia, India, Jubbulpure, Bara Simla Hill.

Orthomerus Seeley, 1883
Hadrosauridae, Ornithopoda
[provisionally considered valid]
Genotype: *dolloi.*
Type: Right femur with imperfect extremities. BMNH 42955.
Upper Cretaceous, Maestrichtian—Europe, Holland, Maastricht.

Oviraptor Osborn, 1924
Ornithomimidae, Coelurosauria
[valid]
Genotype: *philoceratops.*
Type: Skull and jaws, cervical vertebrae, one forelimb. AMNH 6517.
Upper Cretaceous, Djadocta Formation—East Asia, Outer Mongolia, Shabarakh Usu.

Pachycephalosaurus Brown and Schlaikjer, 1943
Pachycephalosauridae, Ornithopoda
[valid]
Genotype: *grangeri.*
Type: Skull. AMNH 1696.
Upper Cretaceous, Lance Formation, Hell Creek Beds—North America, Montana, Carter County, Ekalaka.

Pachyrhinosaurus Sternberg, 1950
Pachyrhinosauridae, Ceratopsia
[valid]
Genotype: *canadensis.*
Type: Skull lacking beak and part of crest. NMC 8867.
Upper Cretaceous, Edmonton Formation—North America, Alberta, Carmongay, Little Bow River.

Pachysauriscus Kuhn, 1959
Teratosauridae, Carnosauria
[to replace *Pachysaurus* Huene, 1908]
Genotype: *ajax* Huene, 1908.
Type: Seventh to thirteenth cervicals, dorsal vertebrae, scapula-coracoid, two humeri, two radii, two ulnae, part of manus, tibia, fibula, fragments of femur. Univ. Tübingen.
Upper Triassic, Keuper, Knollenmergeln—Europe, Germany, Löwenstein.

Pachysaurus Huene, 1908
Teratosauridae, Carnosauria
[preoccupied (Fitzinger, 1843) = *Pachysauriscus* Kuhn, 1959]

Pachyspondylus Owen, 1853
Thecodontosauridae, Prosauropoda
[*nomen dubium fide* Broom, 1911]
Genotype: *orpenii.*

Type: Imperfect vertebra. RCS. Destroyed.
Upper Triassic, Stormberg Series, Red Beds—South Africa, Orange Free State, Harrismith.

Paleosauriscus Kuhn, 1959
Teratosauridae, Carnosauria
[to replace *Paleosaurus* Riley and Stutchbury, 1836—also *nomen dubium*]
Genotype: *platyodon* Riley and Stutchbury.
Type: A single tooth. Bristol Museum.
Upper Triassic, Magnesian Conglomerate—Europe, England, Bristol.

Palaeosaurus Riley and Stutchbury, 1836
Palaeosauridae, Carnosauria
[preoccupied (Geoffry St: Hillaire, 1831)—also *nomen dubium*]

Palaeoscincus Leidy, 1856
Nodosauridae, Ankylosauria
[*nomen dubium*]
Genotype: *costatus*.
Type: A single tooth. ANSP.
Upper Cretaceous, Judith River Formation—North America, Montana, Fort Benton.

Panoplosaurus Lambe, 1919
Nodosauridae, Ankylosauria
[valid]
Genotype: *mirus*.
Type: Skull, jaws, armature, vertebrae, scapula-coracoid, humerus. NMC 2759.
Upper Cretaceous, Belly River Series, Oldman Formation—North America, Alberta, Steveville.

Paracanthodon Huene, 1956
Stegosauridae, Stegosauria
[misspelling of *Paranthodon* Nopcsa, 1929]

Paranthodon Nopcsa, 1929
Stegosauridae, Stegosauria
[*nomen dubium*]
Genotype: *oweni*.
Type: Jaw fragment with teeth. BMNH 47338.
Lower Cretaceous—South Africa, Bushman River below Grahamstown.

Parasaurolophus Parks, 1923
Hadrosauridae, Ornithopoda
[valid]
Genotype: *walkeri*.
Type: Skull, jaws, cervical, dorsal and sacral vertebrae, two forelimbs, pelvis, femur. ROM 768.
Upper Cretaceous, Belly River Series, Oldman Formation—North America, Alberta, Red Deer River, Sand Creek.

Parksosaurus Sternberg, 1937
Hypsilophodontidae, Ornithopoda
[valid]
Genotype: *warreni* Parks, 1926.
Type: Incomplete skull and incomplete skeleton. ROM 804.
Upper Cretaceous, Edmonton Formation, Member B—North America, Alberta.

Paronychodon Cope, 1876
Coeluridae, Coelurosauria
[*nomen dubium*]
Genotype: *lacustris*.
Type: An incisor-like tooth. AMNH 3018.
Upper Cretaceous, Hell Creek Beds—North America, Montana, Judith River.
Remarks: The major group to which the type specimen belongs is an open question.

Parrosaurus Gilmore, 1945
Camarasauridae, Sauropoda
[valid]
Genotype: *missouriensis*.
Type: Thirteen midcaudal centra. USNM 16735.
Upper Cretaceous, Ripley Formation, McNary Sand Member—North America, Missouri, Bollinger County, Glen Allen.

Peishansaurus Bohlin, 1953
Nodosauridae, Ankylosauria
[*nomen dubium*]
Genotype: *philemys*.
Type: Anterior end of right dentary.
Upper Cretaceous—East Asia, China, W. Kansu, Ehr-Chia-Wu-Tung.

Pelorosaurus Mantell, 1850
Cetiosauridae, Sauropoda
[*nomen dubium*]
Genotype: *conybeari*.
Type: Right humerus lacking deltoid

crest. BMNH 28626.
Lower Cretaceous, Wealden—Europe, England, Sussex, Cuckfield.

Pentaceratops Osborn, 1923
Ceratopsidae, Ceratopsia
[valid]
Genotype: *sternbergii.*
Type: Skull and partial skeleton. AMNH 6325.
Upper Cretaceous, Fruitland Formation—North America, New Mexico, San Juan County.

Picrodon Seeley, 1898
Teratosauridae, Carnosauria
[*nomen dubium*]
Genotype: *herveyi.*
Type: A single tooth. BMNH R2875.
Upper Triassic, Rhaetic—Europe, England, Somerset, Wedmore Hill.

Pinacosaurus Gilmore, 1933
Nodosauridae, Ankylosauria
[valid]
Genotype: *grangeri.*
Type: Skull, jaws, and a few dermal bones. AMNH 6523.
Upper Cretaceous, Djadocta Formation—East Asia, Outer Mongolia, Shabarakh Usu.

Pisanosaurus Casamiquela, 1967
Heterodontosauridae, Ornithopoda
[valid]
Genotype: *mertii.*
Type: Right maxilla, right and part of left jaw, nine dorsal and three caudal vertebrae, right tibia, fibula and pes. PVL 2577.
Middle Triassic, Ischigualasto Formation—South America, Argentina, San Juan.

Plateosauravus Huene, 1932
Melanorosauridae, Prosauropoda
[valid]
Genotype: *cullingworthi* Haughton, 1924.
Type: Fragmentary remains of two individuals. SAFM 3341-3356.
Upper Triassic, Stormberg Series, Red Beds—South Africa, Cape Province, Herschel, Kromme Spruit.

Plateosaurus Meyer, 1837
Plateosauridae, Prosauropoda
[valid]
Genotype: *engelhardti.*
Type: Frontal, two dorsal vertebrae, sacrum, two caudals, pubis, femur, tibia. SMNS.
Upper Triassic, Keuper—Europe, Germany, Nürnberg, Heroldsberg.

Platysaurus Agassiz, 1846
Plateosauridae, Prosauropoda
[misspelling of *Plateosaurus* Meyer, 1837]

Pleurocoelus Marsh, 1888
Camarasauridae, Sauropoda
[*nomen dubium*]
Genotype: *nanus.*
Type: Vertebral centra, USNM 4968 dorsal, 4969 and 4970 sacral. All from a very young animal.
Lower Cretaceous, Arundel Formation—North America, Maryland, Prince Georges County, Muir Kirk.

Pleuropeltus Seeley, 1881
Acanthopholidae, Ankylosauria
[=*Struthiosaurus fide* Romer, 1956]

Pneumatoarthus Cope, 1870
Megalosauridae, Carnosauria
[*nomen dubium*]
Genotype: *peloreus.*
Type: Four sacral centra of an immature animal. ANSP 9225.
Upper Cretaceous, Greensand—North America, New Jersey, Monmouth County.

Podokesaurus Talbot, 1911
Podokesauridae, Coelurosauria
[=*Coelophysis fide* Colbert, 1964]
Genotype: *holyokensis.*
Type: Eighteen presacral and 13 caudal vertebrae, coracoid, humerus, manus, pelvis, right hind leg and pes. Destroyed. Cast at Yale.
Upper Triassic, Newark Series, Longmeadow Sandstone—North America, Massachussetts, Hampden County, Holyoke.

Poecilopleuron Fitzinger, 1843
Megalosauridae, Carnosauria
[misspelling of *Poekilopleuron* Eudes-Delongchamp, 1838]

Poecilopleurum Agassiz, 1846
Megalosauridae, Carnosauria

[misspelling of *Poekilopleuron* Eudes-Delongchamp, 1838]

Poekilopleuron Eudes-Delongchamp, 1838
Megalosauridae, Carnosauria
[= *Megalosaurus fide* Romer, 1956]
Genotype: *bucklandi.*
Type: Scapula, humerus, radius, ulna, carpals, phalanges, femur, tibia, fibula, astragaius, nearly complete pes, 21 caudal vertebrae.
Middle Jurassic, Lower Bathonian—Europe, France, Caen, Maladrerie.

Poikilopleuron Owen, 1842
Megalosauridae, Carnosauria
[misspelling of *Poekilopleuron* Eudes-Delongchamp, 1838]

Polacanthoides Nopcsa, 1929
Nodosauridae, Ankylosauria
[*nomen dubium*]
Genotype: *ponderosus.*
Type: Left humerus, left scapula, left tibia. BMNH 1106, 1107, and 2584.
Lower Cretaceous, Wealden—Europe, England, Isle of Wight.

Polacanthus Hulke, 1881
Nodosauridae, Ankylosauria
[valid]
Genotype: *foxi.*
Type: Skeleton lacking skull and fore-limbs. BMNH R175.
Lower Cretaceous, Wealden—Europe, England, Isle of Wight, Barne's Chine.

Polyodontosaurus Gilmore, 1932
Troödontidae, Coelurosauria
[= *Stenonychosaurus fide* D. Russell, 1970]
Genotype: *grandis.*
Type: Left dentary without teeth. GSC 8540.
Upper Cretaceous, Belly River Series—North America, Alberta, Red Deer River, Berry Creek.

Polyonax Cope, 1874
Ceratopsidae, Ceratopsia
[*nomen dubium fide* Marsh, Hatcher, Lull, 1907]
Genotype: *mortuarius.*
Type: Three dorsal vertebrae and fragments of horncores. AMNH 3950.
Upper Cretaceous, Laramie Formation—North America, Colorado.

Poposaurus Mehl, 1915
Poposauridae, Carnosauria
[provisionally considered valid]
Genotype: *gracilis.*
Type: Two dorsal and one caudal vertebrae, left ilium, proximal end of left femur, right femur, distal end of right tibia, shaft of right tibia. FM UR357.
Upper Triassic, Chugwater Formation, Popo Agie member—North America, Wyoming, Fremont County, Lander, Little Popo Agie River.

Priconodon Marsh, 1888
Stegosauridae, Stegosauria
[*nomen dubium*]
Genotype: *crassus.*
Type: A single tooth. USNM 2135.
Lower Cretaceous, Arundel Formation—North America, Maryland, Prince Georges County, Swampoodle.

Priodontognathus Seeley, 1875
Acanthopholidae, Ankylosauria
[*nomen dubium fide* Ostrom, 1970]
Genotype: *phillipsii* Seeley, 1869.
Type: Maxilla fragment. SM B53408.
Lower Cretaceous, Wealden—Europe, England.

Probactrosaurus Rozhdestvensky, 1966
Hadrosauridae, Ornithopoda
[valid]
Genotype: *gobiensis.*
Type: Nearly entire skeleton. PEN AN SSR 2232/1.
Upper Cretaceous, top of lower chalk—East Asia, China, Ala Shan, Maorty.

Proceratops Lull, 1906
Ceratopsidae, Ceratopsia
[to replace *Ceratops,* preoccupied by a *nomen nudum* Rafinesque, 1815]

Proceratosaurus Huene, 1926
Megalosauridae, Carnosauria
[valid]
Genotype: *bradleyi* Woodward, 1910.
Type: Imperfect skull and lower jaw. BMNH R4860.
Middle Jurassic, Bathonian, Great Oolite—Europe, England, Gloucestershire.

Procheneosaurus Matthew, 1920
Hadrosauridae, Ornithopoda

[valid]
Genotype: *praeceps* Parks, 1931.
Type: Skull, vertebrae, right scapula. ROM 758.
Upper Cretaceous, Belly River Series—North America, Alberta, Red Deer River, Sand Creek.

Procompsognathus Fraas, 1913
Procompsognathidae, Coelurosauria
[valid]
Genotype: *triassicus.*
Type: Skull, jaws, two cervical, fourteen dorsal, fourteen caudal vertebrae, scapula-coracoid, radius, ulna, manus, two pubes, two femora, proximal end of tibia, and fibula. SMNS 12591.
Upper Triassic, Stubensandstein—Europe, Germany, Pfaffenhofen.

Prodeinodon Osborn, 1924
Tyrannosauridae, Carnosauria
[*nomen dubium*]
Genotype: *mongoliensis.*
Type: A single tooth. AMNH 6265.
Lower Cretaceous, Aptian, Oshih Formation—East Asia, Mongolia, Oshih.

Prosaurolophus Brown, 1916
Hadrosauridae, Ornithopoda
[valid]
Genotype: *maximus.*
Type: Incomplete skull and jaws. AMNH 5386.
Upper Cretaceous, Belly River Series—North America, Alberta, Steveville, North Fork of Sand Creek.

Protiguanodon Osborn, 1923
Psittacosauridae, Ornithopoda
[valid]
Genotype: *mongoliense.*
Type: Skeleton. AMNH 6253.
Lower Cretaceous, Ondai Sair Formation—East Asia, Mongolia.

Protoceratops Granger and Gregory, 1923
Protoceratopsidae, Ceratopsia
[valid]
Genotype: *andrewsi.*
Type: Skull lacking occiput. AMNH 6251.
Upper Cretaceous, Shamo Series, Djadocta Formation—East Asia, Mongolia, Artsa Bogda, Flaming Cliffs.

Protorosaurus Lambe, 1914
Ceratopsidae, Ceratopsia
[preoccupied Meyer, 1830= *Chasmosaurus* Lambe, 1914]
Genotype: *belli.*
Type: Fused parietals. GSC 491.
Upper Cretaceous, Belly River Series—North America, Alberta, Steveville.

Psittacosaurus Osborn, 1923
Psittacosauridae, Ornithopoda
[valid]
Genotype: *mongoliensis.*
Type: Skeleton. AMNH 6254.
Lower Cretaceous, Oshih Formation—East Asia, Mongolia, Oshih.

Pteropelyx Cope, 1889
Hadrosauridae, Ornithopoda
[*nomen dubium fide* Lull and Wright, 1942]
Genotype: *grallipes.*
Type: Greater part of skeleton without skull or teeth. AMNH 3971.
Upper Cretaceous, Judith River Formation—North America, Montana, Cow Island, 40 mi. below mouth of Judith River on the Missouri River.

Pterospondylus Jaekel, 1913
Podokesauridae, Coelurosauria
[*nomen dubium*]
Genotype: *trielbae.*
Type: Single dorsal vertebra.
Upper Triassic, Upper Keuper—Europe, Germany, Halberstadt.

Rapator Huene, 1932
Coelurosauridae, Coelurosauria
[*nomen dubium*]
Genotype: *ornitholestoides.*
Type: Metacarpal. BMNH 3718.
Lower Cretaceous, Aptian—Australia, New South Wales.

Rebbachisaurus Lavocat, 1954
Camarasauridae, Sauropoda
[valid]
Genotype: *garasbae.*
Type: Right scapula, eleven vertebrae, sacrum, humerus.
Lower Cretaceous, Continental Intercalaire—North Africa, Morocco, Gara Sba.

Regnosaurus Mantell, 1848
Acanthopholidae, Ankylosauria
[*nomen dubium fide* Ostrom, 1970]
Genotype: *northamptoni.*
Type: Fragment of right lower jaw lacking crowns of teeth. BMNH 2422.
Lower Cretaceous, Wealden—Europe, England, Sussex, Cuckfield.

Rhabdodon Matheron, 1869
Iguanodontidae, Ornithopoda
[valid]
Genotype: *priscum.*
Type: Two jaw fragments, one dorsal, two sacral and two caudal vertebrae, right humerus, proximal part of right femur, distal end of right tibia. MNHN.
Upper Cretaceous, Maestrichtian—Europe, France, Provence, Bassin-d' Aix.

Rhaetosaurus Longman, 1925
Cetiosauridae, Sauropoda
[valid]
Genotype: *brownei.*
Type: One cervical, seven dorsal, sacrum, and ten caudal vertebrae, femur, pelvic fragments. Queensland Museum.
Lower Jurassic, Walloon Series—Australia, Queensland, Durham Downs.

Rhodanosaurus Nopcsa, 1929
Acanthopholidae, Ankylosauridae
[=*Struthiosaurus fide* Lapparant, 1947]
Genotype: *lugdunensis.*
Type: Seven dermal plates and one vertebra. Museum de Lyon.
Upper Cretaceous, Maestrichtian—Europe, France, Provence.

Riojasaurus Bonaparte, 1969
Melanorosauridae, Prosauropoda
[valid]
Genotype: *incertus.*
Type: Nearly complete postcranium with skull fragments; PVL 3808.
Upper Triassic, ?Norian. upper section of Los Colorados Formation—South America, Argentina, La Rioja Prov.

Riojasuchus Bonaparte, 1969
Ornithosuchidae, Carnosauria
[valid]
Genotype: *tenuisceps.*
Type: Complete skull with jaws, and large portion of postcranium; PVL 3827.
Upper Triassic, ?Norian, upper portion of Los Colorados Formation—South America, northern Argentina, La Rioja Prov.

Saltopus Huene, 1910
Podokesauridae, Coelurosauria
[valid]
Genotype: *elginensis.*
Type: Partial skeleton. BMNH R3915.
Upper Triassic, Stagonolepsis Sandstone—Europe, Scotland, Elgin, Lossiemouth.

Sanpasaurus Young, 1946
Iguanodontidae, Ornithopoda
[valid]
Genotype: *yaoi.*
Type: Partially articulated skeleton. IVP AS V221, V222.
Upper Jurassic, Tithonian, Kuangyuan Series—East Asia, China, Szechuan, Weiyuan.

Sarcolestes Lydekker, 1893
Stegosauridae, Stegosauria
[valid]
Genotype: *leedsi.*
Type: Lower jaw. BMNH R2682.
Upper Jurassic, Callovian, Lower Oxford Clay—Europe, England, Oxford, Peterborough.

Sarcosaurus Andrews, 1921
Megalosauridae, Carnosauria
[valid]
Genotype: *woodi.*
Type: Vertebrae, pelvis and hind leg. BMNH 4840.
Lower Jurassic, Lower Lias, Bucklandi Zone—Europe, England, Leicestershire, Barrow-on-Soar.

Saurechinodon Owen, 1861
Hypsilophodontidae, Ornithopoda
[to replace *Echinodon* preoccupied]
Genotype: *becklesi* Owen, 1861.
Type: Two fragments of maxillae and two imperfect dentaries. BMNH 48209-12.
Upper Jurassic, Portlandian—Europe, England, Isle of Purbeck.

Saurolophus Brown, 1912
Hadrosauridae, Ornithopoda
[valid]
Genotype: *osborni.*
Type: Nearly complete skeleton. AMNH 5220.
Upper Cretaceous, Edmonton Formation, 500′ below top, Member B—North America, Alberta, Tolman Ferry.

Sauropelta Ostrom, 1970
Acanthopholidae, Ankylosauria
[valid]
Genotype: *edwardsi.*
Type: Partial skeleton, lacking skull. AMNH 3032.
Lower Cretaceous, Cloverly Formation—North America, Montana, Bighorn County, NE¼, Sec. 20, T. 5S, R. 28E.

Sauroplites Bohlin, 1953
Nodosauridae, Ankylosauria
[*nomen dubium*]
Genotype: *scutiger.*
Type: Partial ischium and several dermal plates.
Lower Cretaceous, Oshih equivalent—East Asia, China, Kansu, Tebch.

Saurornithoides Osborn, 1924
Dromeosauridae, Carnosauria
[valid]
Genotype: *mongoliensis.*
Type: Skull, jaws, last four dorsal vertebrae, ventral pelvic elements, incomplete left hind leg. AMNH 6516.
Upper Cretaceous, Djadocta Formation—East Asia, Outer Mongolia, Shabarakh Usu (Bain Dzak).

Scelidosaurus Owen, 1859
Acanthopholidae, Ankylosauria
[valid]
Genotype: *harrisoni.*
Type: Nearly entire skeleton. BMNH R1111.
Lower Jurassic, Lower Lias—Europe, England, Charmouth.

Scolosaurus Nopcsa, 1928
Nodosauridae, Ankylosauria
[valid]
Genotype: *cutleri.*
Type: Nearly entire skeleton. BMNH R5161.
Upper Cretaceous, Belly River Series, Oldman Formation—North America, Alberta, Happy Jack Ferry.

Segisaurus Camp, 1936
Segisauridae, Coelurosauria
[valid]
Genotype: *halli.*
Type: Shoulder girdle, two anterior dorsal and one anterior caudal vertebrae, humerus, radius, ulna, sacrum, pelvis, left hind leg and foot and parts of right. UCMP 32101.
Lower Jurassic, Navajo Sandstone—North America, Arizona, Keet Seel.

Sellosaurus Huene, 1908
Plateosauridae, Prosauropoda
[=*Plateosaurus fide* Romer, 1956]
Genotype: *gracilis.*
Type: Two dorsal, sacrum and all caudal vertebrae, left femur, piece of fibula. SMNS.
Upper Triassic, Stubensandstein—Europe, Germany, Stuttgart, Heslach.

Silvisaurus Eaton, 1960
Acanthopholidae, Ankylosauria
[valid]
Genotype: *condrayi*
Type: Skull, jaws, five cervical, five dorsal, sacrum, and two caudal vertebrae, numerous dermal elements. UKMNH 10296.
Lower Cretaceous, Dakota Formation, Terra Cotta Clay—North America, Kansas, Ottawa County.

Sinocoelurus Young, 1942
Coeluridae, Coelurosauria
[*nomen dubium*]
Genotype: *fragilis.*
Type: Four isolated teeth. IVP AS V232-234.
Upper Jurassic, Tithonian, Kuangyuan Series—East Asia, China, Szechuan, Weiyuan.

Sinosaurus Young, 1948
Ornithosuchidae, Carnosauria
[valid]
Genotype: *triassicus.*
Type: Left maxilla and jaw fragments. IVP AS V34.
Upper Triassic, Lower Lufeng Series—East Asia, China, Yunnan Lufeng.

Smilodon Plieninger, 1846
Teratosauridae, Carnosauria

[preoccupied (Lund, 1842) = *Zanclodon* Plieninger, 1846]
Genotype: *laevis.*
Type: Jaw fragment with four teeth. SMNS.
Middle Triassic, Lettenkohle—Europe, Germany, Wurttemberg, Gaildorf.

Sphenospondylus Seeley, 1883
Iguanodontidae, Ornithopoda
[= *Iguanodon fide* Swinton, 1936]
Genotype: *gracilis* Lydekker, 1888.
Type: Several dorsal vertebrae. BMNH R142.
Lower Cretaceous, Wealden—Europe, England, Isle of Wight.

Spinosaurus Stromer, 1915
Spinosauridae, Carnosauria
[valid]
Genotype: *aegyptiacus.*
Type: Dentary, part of maxilla, two cervical, several dorsal and eight or more caudal vertebrae. Probably destroyed. Not at IPHG.
Upper Cretaceous, Baharije Formation —North Africa, Egypt, Baharije.

Spinosuchus Huene, 1932
Podokesauridae, Coelurosauria
[valid]
Genotype: *caseanus.*
Type: Seven cervical and fifteen dorsal vertebrae. UMMP 7507.
Upper Triassic, Dockum—North America, West Texas, Crosby County.

Spondylosoma Huene, 1938
Thecodontosauridae, Prosauropoda
[provisionally considered valid]
Genotype: *abscondidum.*
Type: Most of vertebral column, scapula, humerus, distal end of femur. Univ. Tübingen.
Middle Triassic, Rio de Rastro—South America, Brazil, Rio Grande de Sul, Chiniqua.

Staurikosaurus Colbert, 1970
Teratosauridae, Carnosauridae
[valid]
Genotype: *pricei.*
Type: Lower jaws, 20 presacral, three sacral, and 35 caudal vertebrae, pelvis, both hind legs lacking feet. MCZ 1669.
Middle Triassic, Santa Maria Formation —South America, Brazil, Rio Grande do Sul, Santa Maria.

Stegoceras Lambe, 1902
Pachycephalosauridae, Ornithopoda
[valid]
Genotype: *validus.*
Type: Frontal-parietal area of skull. NMC 515.
Upper Cretaceous, Belly River Series—North America, Canada, Alberta, Red Deer River.

Stegopelta Williston, 1905
Nodosauridae, Ankylosauria
[valid]
Genotype: *landerensis.*
Type: Fragments of upper and lower jaws, seven dorsal and two caudal vertebrae, sacrum, left tibia, left ulna, left ilium, right pubis, and many bony scutes. FM.
Upper Cretaceous, Cenomanian, Frontier Formation—North America, Wyoming, Fremont County, near Lander.

Stegosaurides Bohlin, 1953
Nodosauridae, Ankylosauria
[*nomen dubium*]
Genotype: *excavatus.*
Type: Two vertebral centra and base of spine.
Upper Cretaceous—East Asia, China, West Kansu, Hui-Hui-Pu.

Stegosaurus Marsh, 1877
Stegosauridae, Stegosauria
[valid]
Genotype: *armatus.*
Type: Fifty to 60 drawers of unprepared material, possibly an entire skeleton. YPM 1850.
Upper Jurassic, Morrison Formation—North America, Colorado, Jefferson County, Morrison, Sec. 26, T. 4S, R. 70W.

Stenonychosaurus Sternberg, 1932
Dromaeosauridae, Carnosauria
[provisionally considered valid]
Genotype: *inequalis.*
Type: Distal end of left tibia, astragulus and pes, first metacarpal, six caudal vertebrae. NMC 8539.
Upper Cretaceous, Oldman Formation—North America, Alberta.

Stenopelix von Meyer, 1857
Psittacosauridae, Ornithopoda
[provisionally considered valid]
Genotype: *valdensis.*
Type: Pelvis and hind legs. Gymnasium in Bückeburg.
Lower Cretaceous, Wealden, Hastings Sand—Europe, Germany, Bückeburg.

Stephanosaurus Lambe, 1902
Hadrosauridae, Ornithopoda
[*nomen dubium*]
Genotype: *marginatus.*
Type: Limb bones, fragments of vertebrae, ribs, teeth. NMC 419.
Upper Cretaceous, Belly River Series—North America, Alberta, Red Deer River.

Stereocephalus Lambe, 1902
Nodosauridae, Ankylosauria
[preoccupied = *Euoplocephalus* Lambe, 1910]
Genotype: *tutus.*
Type: Upper part of heavily armored cranium and a transverse series of 5-keeled scutes. NMC 210.
Upper Cretaceous, Belly River Series—North America, Alberta, Steveville.

Sterrholophus Marsh, 1891
Ceratopsidae, Ceratopsia
[= *Triceratops fide* Hatcher, 1907]
Genotype: *flabellatus.*
Type: Skull, lower jaw, femur, ilium, ischium, scapula, a few vertebrae of a very young individual. YPM 1821.
Upper Cretaceous, Lance Formation—North America, Wyoming, Converse County.

Strenusaurus Bonaparte, 1969
Melanorosauridae, Prosauropoda
[valid]
Genotype: *procerus.*
Type: Seven presacral vertebrae, both scapulocoracoids, ilium, pubis, humerus, femur, portions of right manus, fragments of astragalus and tibia. PVL 3663.
Upper Triassic, ?Norian, upper portion of Los Colorados Formation—South America, northern Argentina, La Rioja Prov.

Streptospondylus von Meyer, 1830
Crocodilian, *non* dinosaurian

Struthiomimus Osborn, 1916
Ornithomimidae, Coelurosauria
[valid *fide* D. Russell, 1972]
Genotype: *altus* Lambe, 1902.
Type: Right hind limb, pubis, and ischium. NMC 930.
Upper Cretaceous, Belly River Series—North America, Alberta, Red Deer River, Berry Creek.

Struthiosaurus Bunzel, 1871.
Acanthopholidae, Ankylosauridae
[valid]
Genotype: *austriacus.*
Type: Posterior half of skull. Geol. Inst. Univ. Vienna, "C."
Upper Cretaceous, Turonian, Gosau Formation—Europe, Austria, Wiener-Neustaadt.

Styracosaurus Lambe, 1913
Ceratopsidae, Ceratopsia
[valid]
Genotype: *albertensis.*
Type: Skull. GSC 344.
Upper Cretaceous, Belly River Series—North America, Alberta, Red Deer River, Berry Creek.

Succinodon Huene, 1941
Diplodocidae, Sauropoda
[provisionally considered valid]
Genotype: *putzeri.*
Type: Jaw fragment with teeth. Probably at University of Tübingen.
Upper Cretaceous, Upper Campanian—Europe, Poland, SE of Warsaw, Canyon of Weichsel River near Bochotnica.

Symphyrophus Cope, 1878
non dinosaurian *fide* Osborn and Mook, 1921
[*nomen dubium*]
Genotype: *musculosus.*
Type: Vertebral centrum and distal end of femur. AMNH 5772.
Upper Jurassic, Morrison Formation—North America, Colorado, Fremont County, Canyon City, Garden Park.

Syngonosaurus Seeley, 1879
Iguanodontidae, Ornithopoda
[*nomen dubium*]
Genotype: *macrocercus.*
Type: A few dorsal vertebrae. SM.
Lower Cretaceous, Greensand—Europe,

England, Cambridge.

Syrmosaurus Maleev, 1952
Nodosauridae, Ankylosauria
[valid]
Genotype: *viminicaudus.*
Type: Much of skeleton. PEN AN SSR 614.
Upper Cretaceous, Lower Cenomanian—East Asia, Mongolia.

Syntarsus Raath, 1969
Podokesauridae, Coelurosauria
[valid]
Genotype: *rhodesiensis.*
Type: Most of postcranium lacking cervical column. Queen Victoria Museum QG/1.
Upper Triassic, Forest Ss.—South Africa, Rhodesia, Nyamandhlovu district, NW of Bulawayo.

Szechuanosaurus Young, 1942
Megalosauridae, Carnosauria
[*nomen dubium*]
Genotype: *campi.*
Type: Teeth. IVP AS V235-36, V238-39.
Upper Jurassic, Tithonian, Kuangyuan Series—East Asia, China, North Szechuan, Kuangyuan.

Talarurus Maleev, 1952
Nodosauridae, Ankylosauria
[valid]
Genotype: *plicatospineus.*
Type: Skeleton with fragmentary skull. PEN AN SSR 557.
Upper Cretaceous, Cenonian—East Asia, Mongolia, Baeen Sheerz.

Tanius Wiman, 1929
Hadrosauridae, Ornithopoda
[valid]
Genotype: *sinensis.*
Type: Nearly entire skeleton.
Upper Cretaceous, Wang Shih Series—East Asia, China, Shantung, Lai Yang Hsien.

Tarbosaurus Maleev, 1955
Tyrannosauridae, Carnosauria
[valid]
Genotype: *bataar.*
Type: Skeleton lacking right forelimb.
Upper Cretaceous, Nemeget Formation—East Asia, Mongolia, Nemegetu.

Tatisaurus Simmons, 1965
Hypsilophodontidae, Ornithopoda
[valid]
Genotype: *oehleri.*
Type: Fragment of left mandible with teeth. CUP 2088.
Upper Triassic, Lower Lufeng Series, Dark Red Beds—East Asia, China, Yunnan, Lufeng, Tati.

Teinurosaurus Cope, 1869
[*nomen nudum*]
Attributing this genus to Cope appears to be a *lapsis calami* on Romer's part (1956, 1966). The name was proposed by Nopcsa (1928) but a type species was not named, so the name is invalid. See: Ostrom, J. H. (1969, Bull. 30, Peabody Mus. Nat. Hist., Yale Univ.: 148.)

Telmatosaurus Nopcsa, 1903
Hadrosauridae, Ornithopoda
[valid]
Genotype: *transylvanicus* Nopcsa, 1900.
Type: Skull.
Upper Cretaceous, Turonian, Gosau Formation—Europe, Hungary, Transylvania.
Remarks: Romer (1956) synonymized this genus, which is based on a skull, with *Orthomerus,* which is based on a femur. Until the same part of each are found the two genera are better left separate.

Tenontosaurus Ostrom, 1970
Iguanodontidae, Ornithopoda
[valid]
Genotype: *tilletti.*
Type: Partial skeleton lacking skull and forelimbs. AMNH 3040.
Lower Cretaceous, Cloverly Formation, Unit VII—North America, Montana, Wheatland County, SW¼, Sec. 26, T. 7N, R. 16E.

Teratosaurus von Meyer, 1861
Ornithosuchidae, Carnosauria
[valid]
Genotype: *suevicus.*
Type: Right maxilla. BMNH 38646.
Upper Triassic, Stubensandstein—Europe, Germany, Stuttgart.

Tetragonosaurus Parks, 1931
Hadrosauridae, Ornithopoda

[=*Procheneosaurus* Matthew, 1920]
Genotype: *praeceps*.
Type: Skull, jaws, cervical, dorsal and sacral vertebrae, right scapula. ROM 3577.
Upper Cretaceous, Belly River Series, Oldman Formation—North America, Alberta, Red Deer River, Sand Creek.

Thecocoelurus Huene, 1926
Coeluridae, Coelurosauria
[*nomen dubium*]
Genotype: *daviesi* Seeley, 1888.
Type: Anterior half of cervical vertebrae. BMNH R181.
Lower Cretaceous, Wealden—Europe, England, Isle of Wight.

Thecodontosaurus Riley and Stutchbury, 1836
Thecodontosauridae, Prosauropoda
[valid]
Genotype: *antiquus* Morris, 1843.
Type: Species based on the remains of several individuals that give good information on the skeleton. Destroyed. Bristol Museum 2.
Upper Triassic, Magnesian Conglomerate—Europe, England, Bristol, Durham Downs.

Thecospondylus Seeley, 1882
Coeluridae, Coelurosauria
[*nomen dubium*]
Genotype: *horneri*.
Type: Natural cast of the neural canal of sacrum. BMNH R291.
Lower Cretaceous, Aptian, Hastings Sand—Europe, England, Kent, Southborough.

Therezinosaurus Maleyev, 1954
Megalosauridae, l.s. (Therezinosauridae, Rozhdestvensky, 1970)
[*nomen dubium*]
Genotype: *cheloniformis*.
Type: Several phalanges.
Upper Cretaceous, Maestrichtian, upper Nemegt beds—East Asia, Mongolia, Gobi Desert, Nemegt Basin.

Thescelosaurus Gilmore, 1913
Hypsilophodontidae, Ornithopoda
[valid]
Genotype: *neglectus*.
Type: Skeleton lacking skull and neck. USNM 7757.
Upper Cretaceous, Lance Formation—North America, Wyoming, Converse County, Doegie Creek.

Thespesius Leidy, 1856
Hadrosauridae, Ornithopoda
[*nomen dubium*]
Genotype: *occidentalis*.
Type: Two caudal centra and one phalanx. USNM 219, 220, 221.
Upper Cretaceous, Lance Formation—North America, South Dakota, Grand River.

Tichosteus Cope, 1877
Incertae sedis
[*nomen dubium*]
Genotype: *lucasanus*.
Type: Immature vertebral centrum. AMNH 5770.
Upper Jurassic, Morrison Formation—North America, Colorado, Fremont County, Canyon City, Garden Park.

Tienshanosaurus Young, 1937
Camarasauridae, Sauropoda
[valid]
Genotype: *chitaiensis*.
Type: Much of skeleton lacking skull. IVP AS.
Lower Cretaceous (basal)—East Asia, China, Sinkiang, Chitai.

Titanosaurus Lydekker (non Marsh), 1877
Diplodocidae, Sauropoda
[*nomen dubium fide* Seeley, 1887]
Genotype: *indicus*.
Type: Two posterior caudal vertebrae. IM.
Upper Cretaceous, Lameta Formation—South Asia, India, Jubbulpure, Bara Simla Hill.
Remarks: On the basis of this material, this genus cannot be defined and consequently it cannot serve as the root of a family name. *Antarctosaurus* should be used as the root for the family name of Cretaceous peg-toothed sauropods, and Diplodocidae (Marsh, 1884) for the entire group.

Titanosaurus Marsh (non Lydekker), 1877
Camarasauridae, Sauropoda
[preoccupied=*Atlantosaurus* Marsh, 1877]

Genotype: *montanus.*
Type: Imperfect sacrum. YPM 1835.
Upper Jurassic, Morrison Formation—North America, Colorado, Jefferson County, Morrison, Sec. 26, T. 4S, R. 70W.

Tornieria Sternfeld, 1911
Diplodocidae, Sauropoda
[to replace *Gigantosaurus* Fraas, 1908]
Genotype: *robusta* Fraas, 1908.
Type: Distal end of right femur, right tibia, right fibula, right pes.
Upper Jurassic, Kimeridgean, Tendaguru Formation—East Africa, Tanzania, Tendaguru.

Torosaurus Marsh, 1891
Ceratopsidae, Ceratopsia
[valid]
Genotype: *latus.*
Type: Skull. YPM 1830.
Upper Cretaceous, Lance Formation—North America, Wyoming, Niobrara County, Lightning Creek.

Trachodon Leidy, 1856
Hadrosauridae, Ornithopoda
[*nomen dubium*]
Genotype: *mirabilis.*
Type: One mandibular tooth. ANSP 9260.
Upper Cretaceous, Judith River Formation—North America, Montana, Judith River.

Triassolestes Reig, 1963
Podokesauridae, Coelurosauria
[valid]
Genotype: *romeri.*
Type: Incomplete skull, lower jaw, and four cervical vertebrae.
Middle Triassic, Ladinian, Ischigualasto Formation—South America, Argentina, San Juan and la Rioja.

Triceratops Marsh, 1889
Ceratopsidae, Ceratopsia
[valid]
Genotype: *horridus.*
Type: Skull and jaws. YPM 1820.
Upper Cretaceous, Lance Formation—North America, Wyoming, Converse County, Buck Creek.

Troödon Leidy, 1856
Coeluridae, Coelurosauria
[*nomen dubium*]
Genotype: *formosus.*
Type: Well-preserved tooth. ANSP 9259.
Upper Cretaceous, Judith River Formation—North America, Montana, Fergus County, Judith River.

Tsintaosaurus Young, 1958
Hadrosauridae, Ornithopoda
[valid]
Genotype: *spinorhinus.*
Type: Posterior part of cranium with nasal processes. IVP AS V725.
Upper Cretaceous, Wangshih Series—East Asia, China, Shantung, Laiyang Basin.

Tyrannosaurus Osborn, 1905
Tyrannosauridae, Carnosauria
[valid]
Genotype: *rex.*
Type: Partial skull, lower jaws, vertebrae, pelvis, and hind limbs. CM 9380.
Upper Cretaceous, Hell Creek Beds—North America, Montana, Dawson County, Hell Creek.

Uintasaurus Holland, 1924
Camarasauridae, Sauropoda
[= *Camarasaurus fide* White, 1958]
Genotype: *douglassi.*
Type: Five posterior cervical vertebrae. CM 11069.
Upper Jurassic, Morrison Formation—North America, Utah, Dinosaur National Monument.

Vectisaurus Hulke, 1879
Iguanodontidae, Ornithopoda
[*nomen dubium*]
Genotype: *valdensis.*
Type: Partial right ilium, BMNH R2497, three dorsal vertebrae, R2494 and 2495, two dorsal neural arches, R2498 and R2499, and a caudal centrum, R2496.
Lower Cretaceous, Wealden—Europe, England, Isle of Wight, Brixton.

Velociraptor Osborn, 1924
Dromaeosauridae, Coelurosauria
[valid]
Genotype: *mongoliensis.*
Type: Skull and jaws, four dorsal, the sacral, and four caudal vertebrae, pubis, ischium, proximal half of left femur, left pes. AMNH 6515.

Upper Cretaceous, Djadocta Formation—East Asia, Outer Mongolia, Shabarakh Usu.

Velocipes Huene, 1932
Podokesauridae, Coelurosauria
[*nomen dubium*]
Genotype: *gürichi.*
Type: Fibula. Staatsinstitut, Hamburg.
Upper Triassic, Middle Keuper—Europe, Germany, Slasks.

Walgettosuchus Huene, 1932
Ornithomimidae, Coelurosauria
[*nomen dubium*]
Genotype: *woodwardi.*
Type: Caudal vertebrae. BMNH 3717.
Lower Cretaceous, Aptian—Australia, New South Wales, Walgett.

Yaleosaurus Huene, 1932
Anchisauridae, Prosauropoda
[=*Anchisaurus fide* Ostrom, 1970]
Genotype: *colurus* Marsh, 1891.
Type: Skull, jaws, eighteen presacral vertebrae, scapula-coracoid, left foreleg and manus, one ilium, pubes, right hind leg and pes. YPM 1883.
Upper Triassic, Newark Series, high in Portland Sandstone—North America, Connecticut, Hartford County, Manchester.

Yaverlandia Galton, 1971
Pachycephalosauridae, Ornithopoda
[valid]
Genotype: *bitholus.*
Type: Frontal region of skull. MIWG 1530.
Lower Cretaceous, Barremian, Wealden Marls—Europe, England, Isle of Wight, Samdown, Yaverland Battery.

Yunnanosaurus Young, 1942
Thecodontosauridae, Prosauropoda
[valid]
Genotype: *huangi.*
Type: Nearly entire skeleton. IVP AS V20.
Upper Triassic, Lower Lufeng Series—East Asia, China, Yunnan, Lufeng.

Zanclodon Plieninger, 1846
Teratosauridae, Carnosauria
[valid *fide* Walker, 1964]
Genotype: *laevis.*
Type: Jaw fragment with four teeth. SMNS.
Middle Triassic, Lettenkohle—Europe, Germany, Gaildorf.

Zapsalis Cope, 1876
Theropoda incertae sedis
[*nomen dubium*]
Genotype: *abradens.*
Type: A single tooth. AMNH.
Upper Cretaceous, Judith River Formation—North America, Montana, Fergus County, Judith River.

Zatomus Cope, 1871
Teratosauridae, Carnosauria
[*nomen dubium*]
Genotype: *sarcophagus.*
Type: A single tooth.
Upper Triassic, Dan River-Deep River Coals—North America, North Carolina, Chatham County.

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FOUR NEW PIRASOCRINID CRINOIDS FROM THE AMES LIMESTONE, PENNSYLVANIAN, OF BROOKE COUNTY, WEST VIRGINIA

J. J. BURKE[1]

INTRODUCTION

A Carnegie Museum collection of Pennsylvanian crinoids from the Ames Limestone, Conemaugh Group, of Brooke County, West Virginia, is of particular interest, as it includes several species that appear to be confined to the Upper Pennsylvanian of the Appalachian region, and for the most part to the Ames Limestone. The Ames is generally regarded as of Upper Missourian age, but documentation of Upper Missourian crinoids is still far from complete. Future exploration may determine the presence of these species in the Pennsylvanian of other regions, in which case they should prove of value for stratigraphic correlation.

While the present paper deals with four new pirasocrinids from the Ames Limestone of Brooke County, West Virginia, treatment of some of the West Virginia forms is supplemented by description of specimens from the Ames of Carroll County, Ohio, which are now deposited in the National Museum of Natural History. Ohio specimens were collected by Ohio University field parties under the supervision of Dr. Myron T. Sturgeon, through whose kindness I was originally afforded an opportunity to study the material.

I wish to express my thanks to the authorities of Ohio University, the National Museum of Natural History (NMNH), and Carnegie Museum (CM) for the privilege of investigating and describing these specimens. I also greatly appreciate the assistance of the West Virginia Geological Survey, which generously supported this project.

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I am grateful to Dr. Robert V. Kesling and Mr. Karoly Kutasi of the Museum of Paleontology, University of Michigan, for the photographs from which the illustrations were made.

SYSTEMATICS

Family Pirasocrinidae Moore and Laudon, 1943

Genus *Plaxocrinus* Moore and Plummer, 1938

Plaxocrinus buffaloensis[2] new species

Figures 1-5

DIAGNOSIS: A fair-sized species: diameter of dorsal cup of holotype 24.1 mm. H/W=0.23. Basal impression moderate; posterior interradius broadly impressed. Interradial notches present. Basals curve downward abruptly from contact with infrabasals; basals and radials slightly convex. Radials not reaching the basal plane and forefacets steeply sloping but not strongly arcuate. Primibrachs with lateral slopes noticeably divergent from spines. Tegmen-roof spines long, slender, and spade-shaped proximally.

TYPES: Holotype CM 33785, a dorsal cup with five primibrachs and portion of one arm retaining five secundibrachs; associated plates include one complete tegmen-roof spine. Paratype NMNH 170558, a dorsal cup with two primibrachs and one secundibrach in association.

OCCURRENCE: Ames Limestone, Conemaugh Group, Upper Pennsylvanian.

LOCALITIES: Holotype CM 33785 from an excavation (Tunnel Road Cut) for West Virginia Route 67 (lat 40°14′24″ N, long 80°35′53″ W) near McKinleyville, Brooke County, West Virginia. Paratype NMNH 170558 from Joe Skinner Quarry, NW¼NE¼ sec. 13 (lat 40°34′20″ N, long 81°01′20″ W), Center Township, about 3 miles east of Carrollton, Carroll County, Ohio.

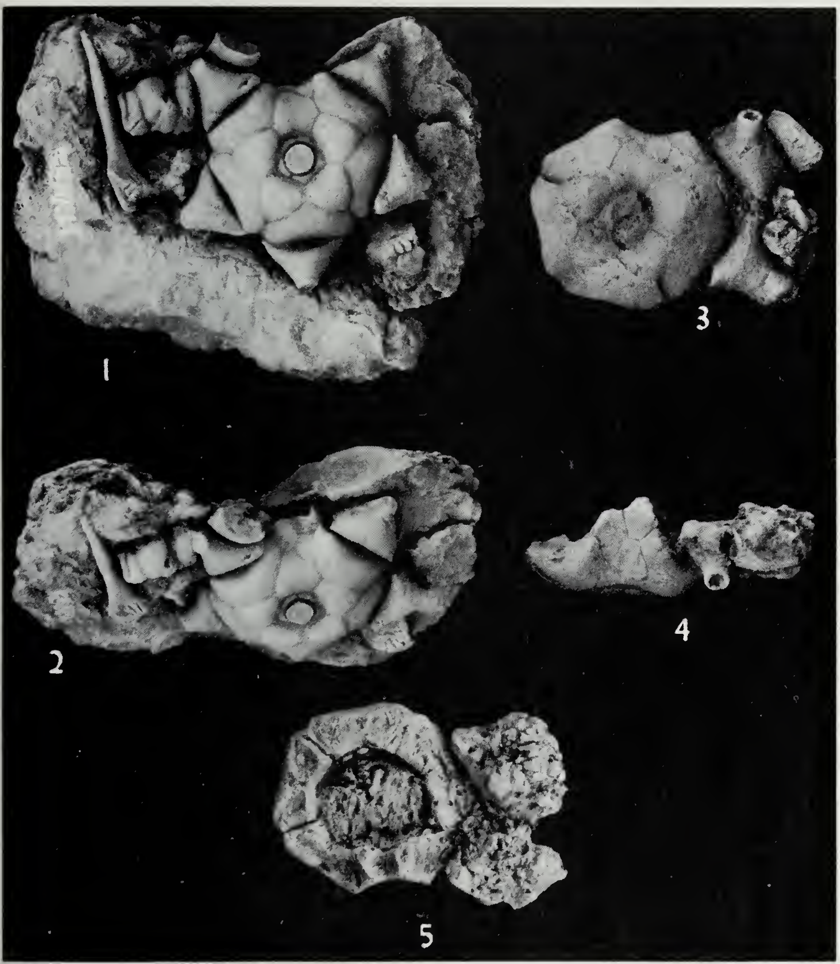
DESCRIPTION: Dorsal cup low, truncate bowl-shaped. Posterior interradius indented; outline of cup irregularly pentagonal in dorsal and ventral view. Cup diameter more than four times the height. Height of basal impression more than one-fourth height of cup; width of impression less than half the diameter of cup. Stem round, culmina about 34, lumen pentalobate. Infrabasals extend well beyond stem impression, curve rather abruptly downward from impression, then more gently upward to meet basals. Basals curve steeply downward proximally, otherwise both basals and radials somewhat convex, especially so in the older specimen, NMNH 170558 (paratype). Plates of both circlets most convex longitudinally. Basals visible in lateral view. Sutures between basals and radials in low hollows in holotype, CM 33785; hollows not evident in paratype NMNH 170558.

Outward and upward slopes of radials terminate in fairly steep, inward-sloping but not strongly arcuate forefacets. Interradial sutures in low hollows; interradial notches present; most prominent in paratype NMNH 170558.

Outward slope of radial articular surface moderate. Outer marginal ridge curved and visible in lateral view, together with outer ligament ridge and relatively short, slit-like outer ligament pit. Interradial notches limit outer facetal area and transverse ridge falls short of full width of plate; ridge denticulate, narrows in vicinity of outer ligament pit, then expands rather abruptly, but narrows to extremeties. Intermuscular notch broad and angular. Intermuscular furrow, in form of broad V, divides muscle areas. Impressed area between triangular intermuscular elevation and transverse ridge.

Radianal intervenes between C radial and CD basal; does not contact BC basal. In holotype, anal X rests on truncate CD basal, separating D radial and radianal. In paratype, anal X also intervenes between D radial and radianal, but barely contacts CD basal where four plates have common juncture at lower lateral angle of D radial. In both

[2] Named for Buffalo Creek, which skirts the locality where the holotype was found.



Figs. 1-5. *Plaxocrinus buffaloensis,* new species. Figs. 1-2, holotype, CM 33785. Fig. 1: dorsal view. Fig. 2: oblique dorsal view showing posterior interradius. Figs. 3-4: paratype, NMNH 170558. Fig. 3: dorsal view. Fig. 4: posterior view. Fig. 5: ventral view. All X 1.

specimens, anal X bears articular faces for IBr_1, tube plate on left, and another tube plate above. In paratype, rt contacts radianal, anal X, and D radial, also bears facets for articulation with IBr_1 on right, together with facets on the left and above for articulation with other tube plates. In the holotype, rt damaged on left; articulation in other areas essentially as in paratype.

$IBrr_1$ axillary and spiniferous; lateral slopes noticeably divergent from spines. Length IBr_1 (C ray of holotype) 4.6 mm, width 9.7 mm; all five spines of $IBrr_1$ of holotype and spines of two $IBrr_1$ associated with paratype broken and in various stages of regeneration. Spine of C-ray IBr_1 of holotype also damaged by boring organism. C- and B-ray $IBrr_1$ of holotype removed for study. Proximal articular facets of $IBrr_1$ much like articular facets of radials, but two channels extend from intermuscular notch to distal surface of each plate. Channels flank sides of strong ridge that divides distal surface into right and left facets, which articulate with IIBrr$_1$. Each channel leads into depression on inner side of denticulate transverse ridge, which intervenes between depression and outer ligament pit. Outer marginal ridges and ligament ridges similar to those of radials, as are articular surfaces adjacent to body chamber, but surfaces on side toward spine reduced and troughlike.

IIBr$_1$ of right arm of D ray displaced; removed for study. Length 3.1 mm, width 7.3 mm. Proximal surface resembles IBr$_1$ surface with which it articulates. Flangelike extension articulates with side of ridge dividing axillary facets of IBr$_1$. Channel leads through fork of intermuscular notch to reach distal surface. Distal surface bears external ligament pit with denticulations external to it and very faint transverse ridge. Short intermuscular furrow reaches to broad intermuscular notch and joins channel, which extends upward from proximal surface. Smooth areas on each side of intermuscular notch give way to broad rugose areas extending to lateral margins.

Left arm of D ray of holotype retains IIBrr$_{1\text{-}5}$. IIBr$_1$ uniserial, quadrangular and appears normal in all respects. IIBrr$_{2\text{-}3}$ cuneate, greatly swollen, apparently represent myzostome galls, having typical myzostome perforation along their common suture. IIBr$_4$ quadrangular, does not extend full width of arm, appears swollen apparently in response to myzostome attack also. IIBr$_5$ extremely slender, rises higher on the right than on left and does not extend full width of arm—essentially a broadly cuneate plate.

Four tegmen-roof plates associated with holotype; one small, hexagonal; three others large, spiniferous. One spiniferous plate complete; spine long (length appr. 24.5 mm) slender, spade-shaped in proximal region, flattened dorsally, bent downward ventrally, showing characteristic coarse canal-like structures.

Holotype retains granulose ornament, mainly on infrabasals and proximal parts of basals, but also along borders of basal and radial sutures and on portions of primibrachs.

TABLE 1. LINEAR MEASUREMENTS OF TYPES, *Plaxocrinus buffaloensis* (IN MM)

	Holotype CM 33785	Paratype NMNH 170558
Height of dorsal cup	5.5	6.1
Width of dorsal cup	24.1	26.6*
Ratio of height to width	0.23	0.23
Height of basal impression	—	1.7*
Width of basal impression	10.2	11.3*
Width of stem impression	4.3	—
Width of infrabasal circlet	6.0	6.4*
Length of basal	5.5(AB)	6.4(AB)
Width of basal	6.4(AB)	7.0(AB)
Length of radial	6.8(B)	7.3(A)
Width of radial	12.0(B)	14.6(A)
Length of suture between basals	2.0	3.1
Length of suture between radials	3.8	5.5
Length of radianal	4.3	6.1
Width of radianal	2.8	4.5
Length of anal X	5.2	7.1
Width of anal X	4.0	4.5
Length of right tube plate	4.9*	5.8
Width of right tube plate	3.2	5.0

*Approximate

Remarks: In size and proportions in general, this species seems to bear closest resemblance to *Plaxocrinus normalis* Strimple (1961). From the latter it appears to differ mainly in having a slightly higher dorsal cup, more convex basals, radials that fail to reach the basal plane, sides of primibrachs more divergent from spines, and more delicate tegmen-plate spines that are less expanded from side to side proximally.

The presumed myzostome infestation of an arm of the holotype is similar to those noted in *Schedexocrinus gibberellus* and *Plaxocrinus normalis* by Strimple (1961). The regenerating primibrach spines are also evidence of injury during life. The breakage of these spines is so uniform as to suggest that they might have been nipped off by some small fish, like *Peripristis semicircularis,* which is associated with these crinoids in the Ames Limestone. The boring on one of the spines, however, might have been a post-mortem occurrence.

Plaxocrinus conemaughensis[3] new species
Figures 6-12

diagnosis: Dorsal cup size about medium for *Plaxocrinus* (known width range 18.0 to 20.8 mm). Cup about four times as wide as high. Posterior interradius impressed. Basal impression relatively shallow; proximal curvature of basals gentle. Basals slightly, radials moderately convex. D radial extends to basal plane. Interradial notches present. First primibrachs spiniferous and axillary. First and second secundibrachs quadrangular, third and fourth cuneate, fifth axillary. Tegmen roof umbrella type. Ornament granulose, confined to infrabasals and proximal portions of basals.

types: Holotype CM 33787, a complete dorsal cup. Paratype CM 33788, dorsal cup with E radial damaged. Paratype CM 33789, basal portion of dorsal cup. Paratype NMNH 170557, part of crown with dorsal cup, portions of arms and parts of tegmen-roof plates.

occurrence: Ames Limestone, Conemaugh Group, Upper Pennsylvanian.

localities: Holotype CM 33787 and paratypes CM 33788 and 33789 from an excavation (Tunnel Road Cut) for West Virginia Route 67 (lat 40° 14′24″ N, long 80° 35′53″ W) near McKinleyville, Brooke County, West Virginia. Paratype NMNH 170557 from Joe Skinner Quarry, NW¼NE¼ sec. 13 (lat 40° 34′20″ N, long 81° 01′20″ W), Center Township, about 3 miles east of Carrollton, Carroll County, Ohio.

description: Dorsal cup low, truncate bowl-shaped, irregularly pentagonal in dorsal or ventral view because of impressed posterior interradius. Cup about four times as wide as high. Height of basal impression about one-half height of cup; width of impression more than one-half diameter of cup in holotype, CM 33787, slightly less than two-fifths that of diameter in large paratype, CM 33788. Stem impression round, showing about 30 culmina in mature specimens, lumen pentalobate. Infrabasal plates curve downward slightly from stem impression, then slightly upward to meet basals. Basals gently convex, most convex longitudinally, visible in lateral view, curve abruptly downward and outward from junction with infrabasals, then upward and outward along cup wall beyond basal plane. Sutures between basals and radials in shallow furrows.

Radials slightly convex, most convex longitudinally. D radial reaches basal plane. (In holotype, B radial, slightly displaced, also reaches basal plane.) Interradial furrows

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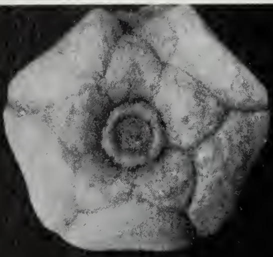
[3] Named for the Conemaugh Group, Pennsylvanian.



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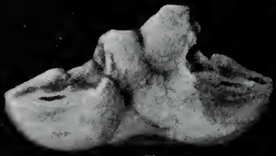

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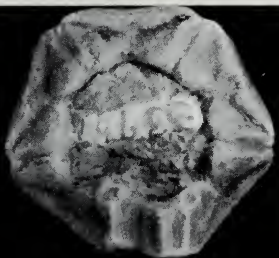

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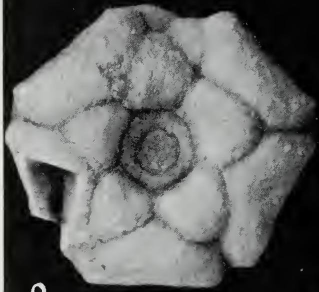

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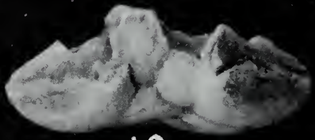

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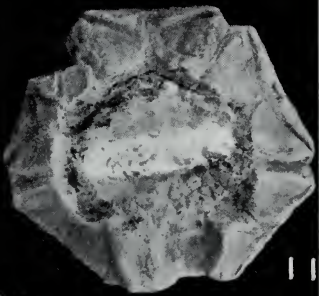

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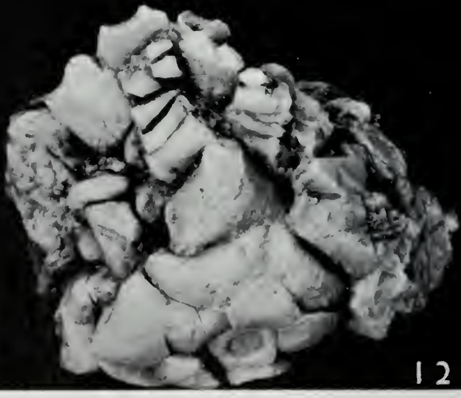

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TABLE 2. LINEAR MEASUREMENTS, DORSAL CUPS, *Plaxocrinus conemaughensis* (IN MM)

	Holotype CM 33787	Paratype CM 33788	Paratype NMNH 170557
Height of dorsal cup	4.6	5.4	—
Width of dorsal cup	18.0	20.8	—
Ratio of height to width	0.26	0.26	—
Height of basal impression	2.0	2.8	—
Width of basal impression	9.6	8.6*	—
Width of stem impression	2.8	3.0	2.6
Width of infrabasal circlet	4.3	5.2	4.7
Length of AB basal	4.0	4.5	4.5
Width of AB basal	4.8	5.1	5.0
Length of A radial	5.3	5.3	5.0*
Width of A radial	9.5	10.6	9.0
Length of suture between basals	1.6	1.5	2.2
Length of suture between radials	3.9	3.9	3.8
Length of radianal	4.5	4.6	4.2
Width of radianal	2.7	2.5	1.9*
Length of anal X	4.3	5.0	—
Width of anal X	2.8	4.0	2.9**
Length of right tube plate	4.5	—	—
Width of right tube plate	3.5	—	—

*Approximate
**Estimated

shallow, but deeper than furrows between basals and radials. Holotype shows interradial notches, notches more conspicuous in large paratype, CM 33788. Forefacet steep, not strongly arcuate, shows some concavity. Radial articular facets face outward. Outer marginal ridge distinct, visible in lateral view, together with external ligament ridge and pit. Ligament pit moderately elongate, not slitlike. Transverse ridge strong, denticulate; narrows in area between external ligament pit and intermuscular depression. Lateral furrows shallow, paralleling transverse ridge. Adsutural slopes moderate. Intermuscular notches broad, more V-shaped in posterior radials. Intermuscular furrows shallow prolongations of notches. Muscle areas broad, lobelike. Plates of posterior interradius normal in paratypes NMNH 170557 and CM 33788, but radianal barely touches BC basal in CM 33788 and in holotype CM 33787. Radianal of holotype meets D radial on left, preventing anal X from contacting CD basal.

Plates of dorsal cup of NMNH 170557 dislocated, but specimen preserves portions of five primibrachs, parts of two arms, and some plates of tegmen roof. All IBrr_1 damaged; spines apparently of medium length. A-ray IBr_1 length 4.7 mm, width 9 mm (est.); plate bears two arms each with four IIBrr; IIBr_4 axillary. IIBr_1 and IIBr_2 uniserial and quadrangular, but IIBr_2 very narrow, its width much greater than length. IIBr_3 cuneate and attenuated, in right ray does not extend full width of arm. IIBr_4 length 1.8 mm, width 3.9 mm; longest side above tip of IIBr_3 wedge. Five or six proximal portions of tegmen-roof spines in place; spines widely spade shaped proximally, flat above, a little convex from side to side below.

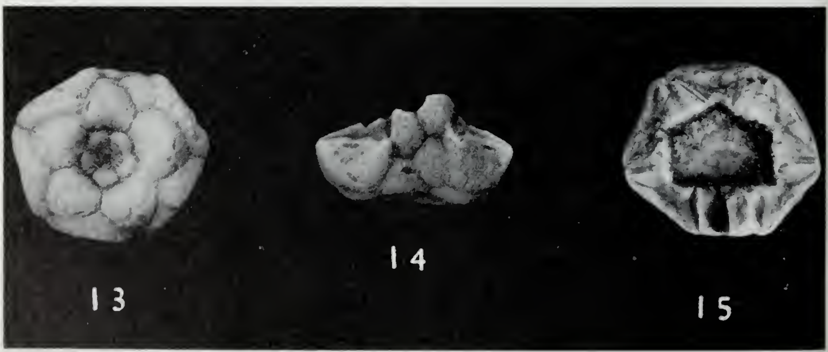
Figs. 6-12. *Plaxocrinus conemaughensis*, new species. Figs. 6-8, holotype, CM 33787. Fig. 6: dorsal view. Fig. 7: posterior view. Fig. 8: ventral view. Figs. 9-11: paratype, CM 33788. Fig. 9: dorsal view. Fig. 10: posterior view. Fig. 11: ventral view. Fig. 12, paratype, NMNH 170557: A-ray view of damaged crown. All X 2.

Ornament finely granulose, confined to infrabasals and proximal regions of basals. Mostly eliminated in preparation of holotype CM 33787 and paratype CM 33788, but well preserved in paratypes NMNH 170557 and CM 33789.

REMARKS: Unfortunately, species of *Plaxocrinus* that compare best with the form under description are known only from dorsal cups. In this respect, *Plaxocrinus conemaughensis* resembles both *Plaxocrinus crassidiscus* Miller and Gurley, 1894, and *Plaxocrinus parilis* Moore and Plummer, 1940. The dorsal cup is sharply distinguished from those of both of the latter species, however, by the slight convexity of its basal plates. It also differs in having the D radial reaching the basal plane. The type specimens of *Plaxocrinus conemaughensis* also exceed known individuals of *Plaxocrinus crassidiscus* and *Plaxocrinus parilis* in size. In general, though, *Plaxocrinus conemaughensis* bears closest resemblance to *Plaxocrinus crassidiscus,* the dorsal cup approaching that of the latter species in (1) the slight depth of its basal impression, (2) lack of angulation between its infrabasal and basal circlets, which characterizes *Plaxocrinus parilis,* (3) showing definite impression of the posterior interradius, and (4) having ornament of identical type and distribution. However, the Conemaugh species differs from *Plaxocrinus crassidiscus* and resembles *Plaxocrinus parilis* in having a relatively lower dorsal cup with less convex radials.

Plaxocrinus amesi[4] new species
Figures 13-15

DIAGNOSIS: A small species: width of dorsal cup (holotype) 13.1 mm. Basal impression moderate. Posterior interradius only faintly impressed. Infrabasals slightly convex; extend well beyond stem impression. Basals mildly convex, relatively large, curve down abruptly from junction with infrabasals. CD and EA basals fail to reach basal plane. Radials more convex than in *Plaxocrinus crassidiscus,* with much less dorsal exposure



Figs. 13-15. *Plaxocrinus amesi,* new species. Holotype, CM 5037. Fig. 13: dorsal view. Fig. 14: posterior view. Fig. 15: ventral view. All X 2.

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[4] Named for the Ames Limestone.

and more arcuate forefacets. Cup plates lack ornament.

TYPE: Holotype CM 5037, a well preserved dorsal cup.

REFERRED SPECIMEN: CM 5039, damaged dorsal cup of young specimen.

OCCURRENCE: Ames Limestone, Conemaugh Group, Upper Pennsylvanian.

LOCALITY: Painters Run (Painter Hollow), lat 40°15′45″ N, long 80°35′33″ W, near Wellsburg, Brooke County, West Virginia.

DESCRIPTION: Dorsal cup of holotype small, truncate bowl-shaped, irregularly rounded in dorsal view, pentagonal in ventral view. Posterior interradius only faintly impressed. Cup about three times wider than high. Basal impression less than one-third height of cup, width of impression about half the width of cup. Stem impression pentagonal, more than half the width of infrabasal circlet, shows about 23 culmina, and slopes downward from pentalobate lumen. Infrabasals very gently convex, slope downward from stem impression, then upward slightly to meet basals. Basals convex, more so longitudinally than transversely, visible in lateral view, curve downward rather abruptly from contact with infrabasals, less steeply outward and upward along cup wall, tend to bend inward at distal tips. CD and EA basals fail to reach basal plane. Interbasal sutures, and sutures between radials and basals, in shallow furrows.

Radials convex in areas bordering cup-plate sutures, least convex transversely. Forefacets prominent, arcuate; extend to about midheight of plates, slope inward steeply to summit of cup. Low furrows mark interradial sutures. Interradial notches barely indicated. Radial articular facets face outward slightly. External marginal ridge bowed, barely distinguishable from external ligament ridge. External ligament pit and both external ridges visible in lateral view of cup; ligament pit slightly elongate, not slitlike. Transverse ridge strong, denticulate; narrows in vicinity of external ligament pit, borders intermuscular depression on inner side. Lateral furrows shallow, run parallel to transverse ridge. Adsutural slopes prominent, not steep. Intermuscular notches wide V-shaped; grade into intermuscular furrows with little distinction; muscle areas triangular.

Plates of posterior interradius (radianal, anal X, and rt) in normal arrangement. Distal extremity of rt extends well beyond distal termination of anal X.

Reference of CM 5039 to species tentative; specimen young, damaged; dorsal cup height 4.8 mm, width 10 mm, height of basal impression 1.6 mm, but cup plates resemble those of holotype; CD and EA basals do not reach basal plane.

TABLE 3. Linear measurements of holotype, *Plaxocrinus amesi,* CM 5037 (in mm)

Height of dorsal cup	4.2
Width of dorsal cup	13.1
Ratio of height to width	0.32
Height of basal impression	1.3
Width of basal impression	6.4
Width of stem impression	2.2
Width of infrabasal circlet	3.8
Length of AB basal	3.5
Width of AB basal	4.0
Length of A radial	4.0
Width of A radial	7.4
Length of suture between basals	1.6
Length of suture between radials	2.2
Length of radianal	3.6
Width of radianal	2.8
Length of anal X	3.2
Width of anal X	2.3
Length of right tube plate	3.0
Width of right tube plate	2.1

REMARKS: This is a smaller species than *Plaxocrinus crassidiscus.* The dorsal cup is relatively higher, the cup plates lack ornament, the stem impression is smaller, the infrabasals are convex rather than flattened, and the basals are relatively larger. In addition, the radials are more reduced and more convex, with more arcuate forefacets that extend to about midheight.

In a previous study (Burke, 1930, unpublished) I identified the holotype of this species and the referred specimen as *Hydreionocrinus discus* Meek and Worthen. The type of *Hydreionocrinus discus* is missing, possibly lost, and I have not been able to make direct comparison of these Ames Limestone specimens with it. In cup height, shape, and proportions of the radials, slight impression of the posterior interradius, and virtual absence of interradial notches, *Plaxocrinus amesi* approaches the Meek and Worthen species. However, those authors note (1860, 1866) that in *Hydreionocrinus discus,* the base (infrabasal circlet) is flat and the subradials (basals) extend "nearly horizontally outward from the base." In these respects, *Hydreionocrinus discus* contrasts sharply with *Plaxocrinus amesi.* These peculiarities of *H. discus* in the basal region of the cup strongly suggest the genus *Anchicrinus* Strimple and Watkins, 1969, however, and I am now convinced that *Hydreionocrinus discus* will eventually prove to be an *Anchicrinus.*

Genus *Anchicrinus* Strimple and Watkins, 1969

Anchicrinus roberti[5] new species

Figures 16-21

DIAGNOSIS: A species resembling *Anchicrinus virginarius* (Moore), new combination, but differing in having a smaller dorsal cup that bears distinctive ornament, has small pits at corners of cup plates, shows no distal impression of the posterior interradius at the summit and lacks interradial notches.

TYPES: Holotype CM 33786, a dorsal cup with damaged D radial and right tube plate lost. Paratype CM 5038, a worn dorsal cup lacking the E radial.

OCCURRENCE: Ames Limestone, Conemaugh Group, Upper Pennsylvanian.

LOCALITIES: Holotype CM 33786 from Tunnel Road Cut, an excavation for West Virginia Route 67 (lat 40°14′24″ N, long 80°35′53″ W) near McKinleyville, Brooke County, West Virginia. Paratype CM 5038 from Painters Run (Painter Hollow), (lat 40° 15′45″ N., long 80°35′33″ W), near Wellsburg, Brooke County, West Virginia.

DESCRIPTION OF HOLOTYPE: Dorsal cup small, truncate bowl-shaped, pentagonal in ventral view, rounded pentagonal in dorsal view, somewhat more than three times as wide as high. Basal impression extremely shallow, less than 1 mm in height, slightly less than half the cup diameter in width. Posterior interradius slightly impressed proximally. Infrabasals essentially flat; width of infrabasal circlet nearly twice that of pentagonal stem impression. Basals with slight curvature downward from juncture with infrabasals; plates only slightly convex, visible in lateral view, with sharpest curvature beyond basal plane; all basals tending to be slightly impressed at distal extremities. CD basal elongate, least convex, does not reach basal plane.

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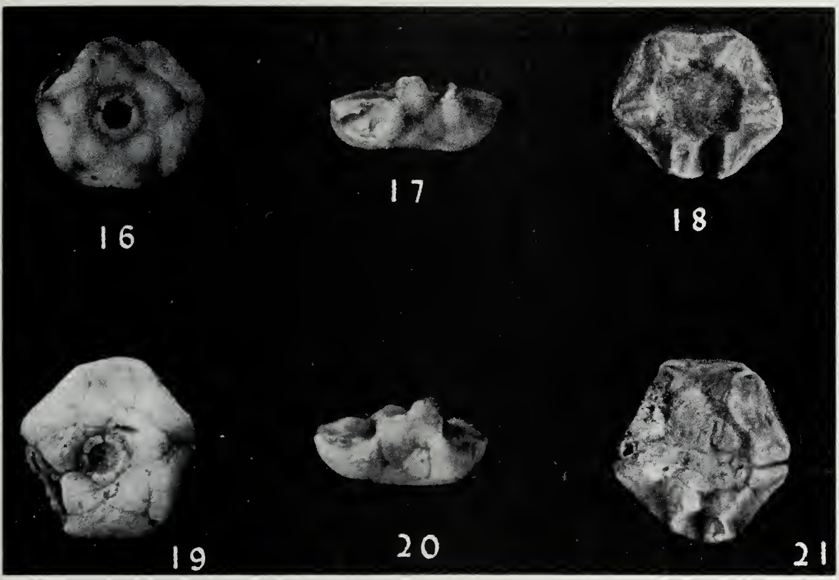
[5] Named for my brother, Robert, in appreciation of his help in collecting crinoids from the Ames Limestone.



Figs. 16-21. *Anchicrinus roberti,* new species. Figs. 16-18, holotype, CM 33786. Fig. 16: dorsal view. Fig. 17: posterior view. Fig. 18: ventral view. Figs. 19-21, paratype, CM 5038. Fig. 19: dorsal view. Fig. 20: posterior view. Fig. 21, ventral view. All X 2.

Beyond proximal tips of radials, sutures between basals and radials in shallow furrows. Radials strongly convex proximally and along sides, most convex transversely, proximal tips in basal impression, corners of plates indented at junctions with distal tips of basals. Hollows bound interradial sutures proximally; hollows absent distally. Interradial notches also absent. Prominent, steep, lunate forefacet extends downward from superior corners of radial to well below midheight of plate, sloping upward and inward to radial summit. Forefacet abruptly terminates outward slope of radial, contributing to pentagonal outline of cup in dorsal view. Radial facets face outward moderately; details poorly preserved. Outer marginal ridge, outer ligament ridge and outer ligament pit face outward; ridges curved, ligament pit elongate but not slitlike. Transverse ridge strong, but finer features obliterated. Lateral furrows obscure, but indicated. Adsutural slopes prominent; muscle areas face outward. Intermuscular notches V-shaped in posterior radials, broader in other radials.

Anal X and radianal still in place; rt missing. Anal X rests on truncated tip of CD basal below; on left abuts against D radial and bears facet for IBr_1, shows facet above for articulation with tube plate, on right carries facet for rt and rests against radianal. Radianal in normal contact with BC radial below and with C radial on right, but greatly attenuated distally; barely meets with rt.

Pits or dimples at corners of anal plates similar to those marking tips of basals at junctions with interradial sutures. All plates of cup ornamented with fine, glistening angular granulations.

COMPARISON WITH PARATYPE: Paratype CM 5038, a larger (and older) individual than holotype specimen, CM 33786; E radial missing and cup plates worn, but right tube plate (absent in holotype) preserved. Characteristic ornament still remains on some infrabasals and plates of posterior interradius; some pits at corners of plates also preserved. Actual height of cup less than that of holotype, and cup nearly four times wider than high.

Basal impression shallow, as in holotype, but all cup plates less tumid; hollows along sutures between radials and basals almost obliterated. Radials with gentler slopes and greater exposure in dorsal view; forefacets steep, but much less extensive and less arcuate.

Radial facets facing outward much more steeply than in holotype. Transverse ridges better preserved; ridge shows denticulations and narrows to form border or prominent intermuscular depressions. Lateral furrows shallow, broad; extend parallel to transverse ridge.

Plates of posterior interradius show normal arrangement; rt makes broad contact with radianal.

Measurements of types are summarized below.

TABLE 4. Linear measurements, *Anchicrinus roberti* (in mm)

	Holotype CM 33786	Paratype CM 5038
Height of dorsal cup	3.6	3.0
Width of dorsal cup	11.3	11.7
Ratio of height to width	0.33	0.26
Height of basal impression	0.8	1.0
Width of basal impression	5.0	5.8
Width of stem impression	1.8	2.2
Width of infrabasal circlet	3.2	3.2
Length of AB basal	2.7	2.8
Width of AB basal	3.1	3.3
Length of A radial	3.5	3.5
Width of A radial	5.9	6.2
Length of suture between basals	0.9	1.1
Length of suture between radials	2.4	2.3
Length of radianal	3.8	3.2
Width of radianal	1.4	2.0
Length of anal X	3.0	3.1
Width of anal X	2.4	2.6
Length of right tube plate	—	3.4
Width of right tube plate	—	2.5

REMARKS: This little species is quite evidently congeneric with *Anchicrinus toddi* Strimple and Watkins (1969), showing a shallow basal concavity, gently convex basals, and a tendency for the proximal tips of the radials to extend into the basal impression—all characteristic of *Anchicrinus.* However, except as noted in the diagnosis, the dorsal cup of *Anchicrinus roberti* also resembles that of a specimen described by Moore (1939) as *Plaxocrinus virginarius.* The latter is evidently another representative of the Strimple and Watkins genus, for which I propose the designation *Anchicrinus virginarius* (Moore), new combination.

Previously (Burke, MS, 1930) I identified the paratype of *Anchicrinus roberti,* CM 5038, as *Hydreionocrinus discus* Meek and Worthen,

1860. The Meek and Worthen species may also prove to be an *Anchicrinus,* as I have indicated above in connection with *Plaxocrinus amesi,* but *H. discus* differs from *Anchicrinus roberti* not only in being an unornamented form, but also in showing differences in arrangement and proportions of the anal plates that are probably significant at the species level.

REFERENCES CITED

MEEK, F. B., AND A. H. WORTHEN
1860. Descriptions of new species of Crinoidea and Echinoidea from the Carboniferous rocks of Illinois and other western states: Proc. Nat. Acad. Sci. Philadelphia 4:379-397.
1866. Description of invertebrates from the Carboniferous system: Illinois Geol. Surv. 2:143-411, pl. 14-32.
MILLER, S. S. AND W. F. E. GURLEY
1894. Descriptions of some new species of invertebrates from the Paleozoic rocks of Illinois and adjacent states: Illinois State Mus. Nat. Hist. Bull. 3:1-81, pl. 1-8.
MOORE, R. C.
1939. New crinoids from Upper Pennsylvanian and Lower Permian rocks of Oklahoma, Kansas and Nebraska: Denison Univ. Bull. 39 Jour. Sci. Lab. 34:171-279, pl. 5-9.
MOORE, R. C. AND F. B. PLUMMER
1940. Crinoids from the Upper Carboniferous and Permian strata in Texas: Texas Univ. Bull. 3945:1-468, pl. 1-21.
STRIMPLE, H. L.
1961. Late Desmoinesian crinoid faunule from Oklahoma: Oklahoma Geol. Bull. 93:1-189, pl. 1-19.
STRIMPLE, H. L. AND W. T. WATKINS
1969. Carboniferous crinoids of Texas with stratigraphic implications: Paleont. Americana 6(40):1-275, pl. 1-56.

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NEW PTEROMALIDAE OF THE *DIBRACHYS* GROUP (HYMENOPTERA: CHALCIDOIDEA) WITH A KEY TO GENERA

George E. Wallace
Curator, Section of Insects and Spiders

The following new Pteromalidae are closely allied to a number of genera which, in the catalogs and taxonomic works treating the family, are usually placed or "keyed out" in close proximity to each other. I have chosen to refer to this assemblage as the *Dibrachys* Group, the largest included genus being *Dibrachys* Förster.

Below the generic level at least, this paper is not intended to be revisionary in scope.[1] Treatment therefore is confined to a diagnosis of the group, descriptions of the new species and genus, presentation of a key to the genera, and a check list of those species whose names at present are in good standing. Biological information and synonymies for the majority of the species have been so well documented (Peck 1951, Burks 1958, Peck 1963, Burks 1967, Graham 1969) in recent years that I see no reason to repeat such material here. The general known distribution, however, is given for each species, and also any host information that is available for newer species.

I am grateful to Dr. B. D. Burks, Systematic Entomology Laboratory, USDA, U. S. National Museum, for the loan of specimens on which the descriptions are based, and for more instances of help and advice than can be enumerated here. To Dr. Oswald Peck, Canada Department of Agriculture, I am indebted for many helpful comments and criticisms. It is fitting also to acknowledge my indebtedness to the recent monumental work of Dr. M. W. R. de V. Graham (1969) which has been a guide to several taxonomic characters that I had not included in this

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[1] Aside from the inclusion of the North American genus *Systellogaster* Gahan, and the new genus herein described, there is nothing innovative in the arrangement of the genera. As far as I am aware, *Systellogaster* has never previously been included in a generic key.

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paper in its early stages. Barbara J. Robertson executed the drawings for figures 1-4.

DIAGNOSIS, *Dibrachys* GROUP

Postmarginal vein short, approximately as long as, or shorter than, the stigmal—never much longer; their combined lengths (measured from their common base) much shorter than the width of the wing, usually about one-half this width. Combined marginal and post-marginal veins usually shorter than the wing width measured from the base of the marginal. Wing-fringe usually absent, at least from apex of postmarginal vein to wing apex. Antennae placed on, or close to, a line connecting the ventral margins of the eyes; face more or less receding below. Eyes bare or nearly so. Mandibles never both distinctly 3-dentate; usually the right clearly 4-dentate, the left 3- or 4-dentate or intermediate by broadening or forking of third tooth. Pronotum never as wide as mesonotum. Posterior tibiae one-spurred. Propodeum without a well-developed nucha, and without a spur-like projection at each side. Pygostylar bristles subequal. Hind margins of gastral terga not incised at middle.

Family Pteromalidae; Subfamily Pteromalinae

Genus **Helocasis,** new genus

FEMALE: Head large, wider than thorax by ratio of 10:7, higher than wide by same ratio; vertex broad; temples not receding; occiput excavated, acarinate. Eyes bare, ratio of length (longest diameter) to width 3:2. Antenna (fig. 4): formula 11263; inserted slightly above a line connecting lower margins of eyes; scape sub-cylindrical, extending slightly above the median ocellus; pedicel longer than the two ring-segments combined, longer than the first funicular segment, but shorter than all three combined; funicular segments from 1 to 6 increasing only gradually in width and length, club apex sharp. Face below the antennal insertions bearing a prominent nose-like projection overhanging the clypeus (figs. 1 & 2). Antennal scrobe cavity rather deep basally, but becoming shallower upwardly, disappearing just below the median ocellus. Clypeus extremely reduced, the anterior margin slightly produced medially; sides of the face flanking the clypeus somewhat protuberant; malar sulcus absent; genae slightly excavated. Mandibles robust, each with an arcuate fold medially (fig. 1), the ends of the fold especially prominent, the upper end a conspicuous knob that slightly overlaps the clypeus. Left mandible with three distinct teeth, the outer two acute, the inner broad and slightly concave at apex; (dentition of right mandible not examined). Pronotum striately punctate except for a narrow shiny band along the close-fitting posterior edge; anterior face declivitous, the carina poorly defined. Notaulices incomplete. Scutellum without a cross-furrow. Legs normal. Postmarginal and stigmal veins equal in length, each shorter than one-half the marginal, the latter slightly broadened at base (fig. 3); wing fringe short—on three (of four forewings) the fringe of the anterior apical half is lacking (probably rubbed off). Posterior border of metanotum divided at middle third into two thin carinae separated by a row of punctures, the anterior carina forming a narrow shelf behind the scutellum. Propodeal surface uneven, reticulately punctate, a pit on each side setting off the short broad neck; spiracle reniform, anteriorly contiguous to the metanotum; median and lateral carinae present; the median distinct, sinuate; each lateral carina divaricated posteriorly, the outer branch recurved anteriorly, inclosing a sulcus that almost surrounds the spiracle; width of this sulcus and diameter of spiracle subequal, floor of sulcus finely and delicately punctate. Abdomen rotund, flat, equal to thorax in length.

MALE: Unknown.

TYPE SPECIES: *Helocasis burksi,* n. sp.

Helocasis burksi, new species
Figures 1-4

FEMALE: Length 2.0-2.1 mm. Head and thorax reticulately punctuate, punctures finer on the scutellum, widened transversely on the pronotum. Head sparsely furnished with stout hairs—most abundant on the genae, at each side of the nose-like projection, and on the mandibles. Postocellar and ocellocular lines subequal. Median ocellus appreciably larger than the lateral ocelli. Lengths of veins of forewing (submarginal: marginal: postmarginal: stigmal) in ratio of 11:7:3:3. First abdominal tergum approximately as long as one-third of abdomen, the hind margin slightly convex-arcuate; following terga approximately equal to one-third of first.

Color of head and thorax black, the scutellum slightly cupreous; abdomen brown. Antennae brown. All coxae black tinged with castaneous; remaining parts of all legs brown. Wings hyaline.

Described from two specimens.

MALE: Unknown.

HOST: Unknown.

TYPE LOCALITY: Presque Isle, Erie, Pa.

Holotype and paratype in United States National Museum of Natural History Chalciodoidea Collection. The holotype is labeled: ferns behind lab; Presque Isle, Erie, Pa. vii-31-1934 G. E. Wallace. The paratype is labeled: Muncie, Ill. Sept. 10, 1936 Cattail Bog B. D. Burks. The specimen that I collected was taken by sweeping ferns at the end of a wet meadow. Dr. Burks has told me that his specimen was probably taken by sweeping cattails.

Genus *Systellogaster* Gahan
Systellogaster gahani, new species

FEMALE: Length 2.15-2.30 mm. Antennae essentially as in *S. ovivora.* Vertex, temples, and genae reticulately punctate. Face, lower fifth of frons, mesoscutum (including scapulae) anteriorly, and pronotum finely and densely punctate. Scutellum, axillae, more than posterior half of the mesoscutum, and upper portion of frons glassy smooth. These polished areas, particularly of frons, with minute punctures marking sites of obsolescent or rubbed-off hairs. Propodeum closely punctate, callus slightly flared laterally over coxal insertions. Petiolar emargination deep, nucha evident only as a flange on either side of abdominal petiole. Lengths of submarginal, marginal, postmarginal, and stigmal veins in ratio of 7:5:1:1. Abdomen rotund, first tergum approximately one-fourth length of abdomen, the remaining terga subequal.

Head black, temples with slightly greenish reflections. Pronotum, mesonotum, and scutellum black, the latter two with coppery reflections—the reflections especially evident on the scutellum; pronotum with a greenish cast. Propodeum blue. Dorsoposterior edge of hind coxae bluish-purple; remainder of hind coxae, fore- and mid-coxae, and all femora and tibiae, completely brown; tarsi stramineous. Forewings behind stigmal and marginal veins with a tawny cloud, extending beyond these veins apically and basally, and becoming fainter apically, disappearing at about middle of wing. Abdomen brown.

REMARKS: Set off markedly from *ovivora,* the other species of the genus, by the highly polished impunctate areas of head and thorax.

Described from three specimens.

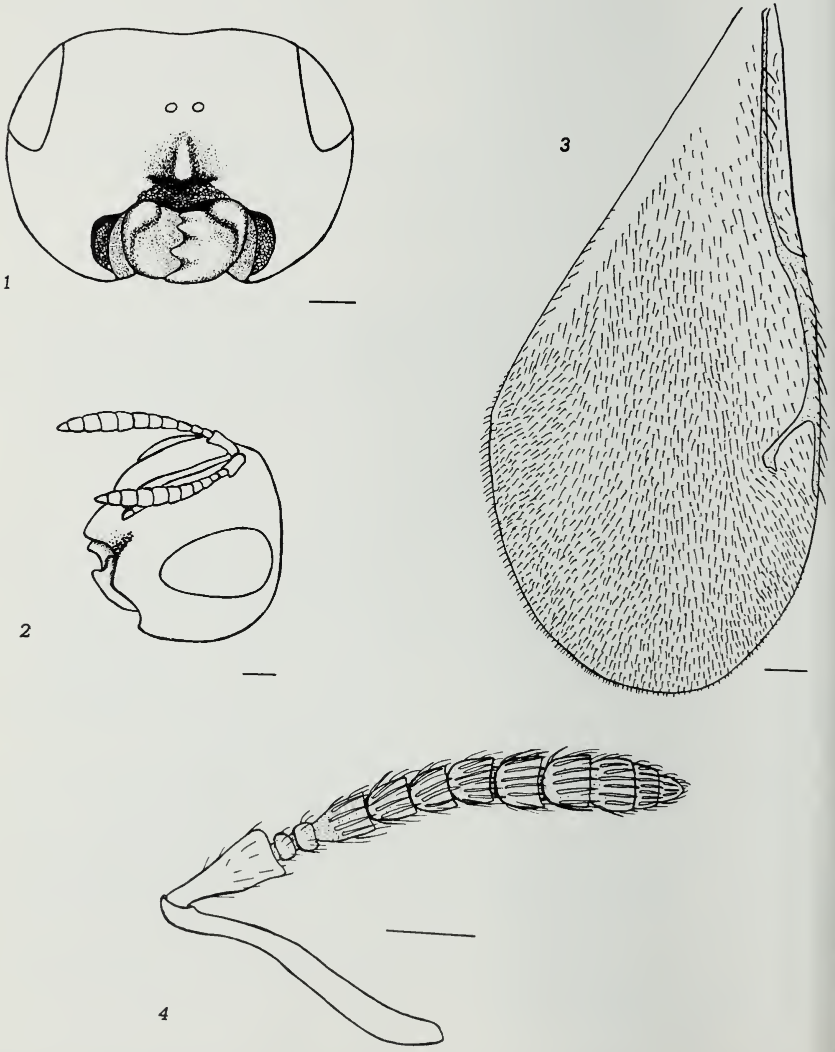
MALE: Unknown.

HOST: Unknown.

Holotype and one paratype in United States National Museum of Natural History Chalcidoidea Collection. The holotype is labeled: W. S. Craig, Coll., Columbia, Mo. 4-14-40.

The paratype bears the same data.

One paratype in Illinois Natural History Survey Chalcidoidea Collection. Labeled: Illinois Natural History Survey Collection #17652,—Urbana, Ill., Oct. 24, 1891, woods, Hart. This paratype and the holotype bear Gahan det. labels to genus, and "n. sp.".



Figs. 1-4: *Helocasis burksi,* new species. (All scale lines equivalent to 0.1 mm) Fig. 1. Head, lower front view. Fig. 2. Head, quarter view. Fig. 3. Right forewing. Fig. 4. Antenna.

KEY TO GENERA OF THE *Dibrachys* GROUP

1. Head thin antero-posteriorly. Thorax dorsally flattened . . . . *Platneptis* Bouček
Not at all as above 2

2. Pronotum with an anterior carina; if carina weakly indicated, then a distinctly impressed scutellar crossfurrow present, the funicular segments sometimes transverse. Antenna with one or two ring-segments 3
Pronotum without an anterior carina. Antenna with two or three ring-segments 6

3. (2). Occiput with a carina; if carina weakly indicated, then funicular joints transverse. Genae rounded 4
Occiput without a carina; funicular segments not transverse. Genae excavated 5

4. (3). Marginal vein swollen at base. Antenna placed slightly above subocular line; *female* with one ring-segment and seven funicular segments, the latter not transverse; *male* with two ring-segments and six funicular segments; club apex not acutely pointed. Pronotum bearing a row of rather long recumbent brown hairs. Wing fringe frequently absent (sometimes obsolete) from wing apex to end of postmarginal vein . . . . *Muscidifurax* Girault
Marginal vein evenly wide throughout. Lower edge of toruli touching subocular line. Antenna of both female and male with two ring-segments and six funicular segments; funicular segments of female transverse. Intervals between pronotal hairs equal to or more than lengths of individual hairs. Propodeal callus moderately hairy; nucha prominent; lateral carinae, and usually the median carina, present. Wings without fringe; the wings of *male* abbreviated. Antennal club not acutely pointed . . . . *Nasonia* Ashmead

5. (3). Head large, thick, much wider than the thorax; vertex usually thick antero-posteriorly, flattened, meeting occiput at an angle; occiput excavated. Propodeal callus-hairs abundant. Wing fringe absent. Abdomen conic-ovate, longer than the thorax. Scutellar cross-furrow indicated only by a line and a slight change of sculpture and color. Eye measured vertically rather long, tapering at lower half . . . . *Dibrachoides* Kurdjumov
Head smaller, the vertex more rounded. Scutellum with a distinctly impressed cross-furrow. Propodeal callus sparsely haired. Abdomen rotund. Wing fringe absent . . . . *Schizonotus* Ratzeburg

6. (2). Occiput either with a carina, or the occiput-vertex boundary distinctly angulate 7
Occiput without a carina; occiput and vertex not meeting at an angle 9

7. (6). Occiput with a carina. Abdomen usually (all North American species) conic-ovate, longer than the thorax. Punctures normal in size—3 to 5 in a .025 x .025 mm square. Wing fringe usually either absent or only scantily present on posterior edge of wing; present only in *Dibrachys daphne* Girault . . . . *Dibrachys* Förster
Occiput without a carina; occiput-vertex boundary angled. Abdomen ovate, shorter than the thorax. Punctures either normal in size or extremely fine 8

8. (7). First funicular segment not subconical, all funicular segments subequal in length; antennae inserted above the lower margin of the eyes. Punctures small, dense—9 or 10 in a .025 x .025 mm square. Lower face densely and

uniformly punctate, the punctures effacing the clypeal boundary; malar sulcus absent. Rarely the posterior half of mesoscutum, scutellum, and axillae impunctate and highly burnished. Marginal vein long, exceeding the width of wing (as measured across from the base of vein); a little more than three times the length of the postmarginal; postmarginal and stigmal veins short, subequal. Wings infumate. Hair patch on propodeal callus small, but conspicuous . . . . *Systellogaster* Gahan

First funicular segment subconical, about as long as second and third combined. Punctures normal. Scutellum without a cross-furrow. Genae excavated at bases of mandibles. Either postmarginal or stigmal vein more than one-half as long as marginal vein . . . .*Conomorium* Masi

9. (6). Abdomen rotund or subrotund. Antennae usually placed slightly below the subocular line; face sometimes receding below antennae. Occiput excavated; vertex long, but not meeting occiput at an angle. Pedicel shorter than first funicular and ring-segments combined 10

Abdomen not rotund or subrotund. Antennae placed below the subocular line. Face receding below antennae. Occiput-vertex boundary not angulate. Pedicel longer than first funicular and ring-segments combined. Wings clear or infumate . . . . *Tritneptis* Girault

10. (9). Marginal vein nearly four times as long as the stigmal. *Male* scape greatly enlarged, deeply incised subapically. (I have seen only males.) . . . . *Stichocrepis* Förster

Not at all as above 11

11. (10). Antennae with two ring-segments, inserted at or well below the subocular line; face strongly receding below antennae. Wings sometimes infumate. Face without a nose-like projection below the antennae. Marginal vein of uniform width throughout . . . . *Kranophorus* Graham

Antenna with three ring-segments, or the face with a nose-like projection below the antennae. Antenna inserted above the subocular line. Club apex rather pointed. Wings clear 12

12. (11). Antenna with three ring-segments. Face without a prominent nose-like projection. Marginal vein of uniform width throughout; postmarginal and stigmal veins subequal in length. Wing fringe indistinct at least on anterior half of apical border 13

Antenna with two ring-segments. Face with a prominent nose-like projection below the antennal insertions. Basal half of marginal vein somewhat broadened. Wing fringe short, especially along anterior half of apical border where the fringe is probably lacking (rubbed off) on older individuals . . . . *Helocasis* Wallace

13. (12). Marginal vein at least twice as long as radius; antenna attached below level of ventral eye margin, where face convex and strongly receding towards mouth. . . . . *Pseudomicromelus* Gahan and Fagan

Marginal vein at most 1.5 times as long as radius; antenna attached at level of lower eye margin, where face not strongly prominent . . . . *Cyclogastrella* Bukovskij

Note: Characters of couplet 13, separating *Pseudomicromelus* from *Cyclogastrella*, are from Peck, Bouček, and Hoffer, 1964. The key characters for *Platneptis* and *Conomorium* are from this work, and from Graham, 1969. I have not seen representatives of these last two genera.

CHECKLIST OF GENERA AND SPECIES

Conomorium Masi. One species, *C. patulum* (Walker).
Known distribution: Europe.

Cyclogastrella Bokovskij. Three species.
(1) *Cyclogastrella clypealis* Bouček.
Known distribution: Eastern Europe (recorded only from Czechoslovakia and Moldavian SSR).
(2) *C. deplanata* (Nees)
Known distribution: North America, Europe, North Africa (recorded only from Morocco).
(3) *C. flavius* (Walker)
Known distribution: Northern Europe, including Britain.

Dibrachoides Kurdjumov. Two species.
(1) *Dibrachoides dynastes* (Forster).
Known distribution: North America, Europe, North Africa.
(2) *D. cionobius* Graham.
Known distribution: Europe (recorded only from England).

Dibrachys Förster. Fourteen (?) species. A key to six species is provided by Bouček (1965), and Graham (1969) gives a key to eight. The subgenera, where given here, are according to these authors.
(1) *Dibrachys (Allodibrachys) affinis* Masi.
Known distribution: Western Europe including Britain; North Africa (Algeria).
(2) *D. (D.) boarmiae* (Walker).
Known distribution: England.
(3) *D. (D.)* braconidis (Ferriere and Faure).
Known distribution: Italy (Viggiani 1968: 112-113); France.
(4) *D. (D.)* cavus (Walker).
Known distribution: Holarctic. Probably will be found elsewhere.
(5) *D. confusus* (Girault).
Known distribution: The holotype was collected at Washington, D.C.; but see remarks under *D. maculipennis* Szelenyi.
(6) *D. daphne* Girault.
Known distribution: California.
(7) *D. (D.) fuscicornis* (Walker).
Known distribution: Britain.
(8) *D. (Allodibrachys) hians* Bouček.
Known distribution: Italy (Viggiani (1968: 113-114); Czechoslovakia, Moldavian SSR.
(9) *D. (D.) lignicola* Graham.
Known distribution: England, Ireland.
(10) *D. (D.) maculipennis* Szelenyi.
Known distribution: Hungary. Also N. A. (Hobbs, 1968, and Peck, 1969).
(Note: Dr. B. D. Burks believes that this is a synonym of *D. confusus* Girault, *in litt.*).
(11) *D. (D.) saltans* (Ratzeburg). Discussed but not keyed by Graham (1969: 809).
Known distribution: Holarctic.
(12) *D. (D.) vesparum* (Ratzeburg). Discussed but not keyed by Graham *(loc. cit.)*.
Known distribution: Europe.

Of doubtful standing:

(13) *D. antiqua* (Walker). Only reference seen: Nielsen (1965: 54, 56).
Host: Parasitizes *Rhacodineura antiqua* Mg. (Diptera: Tachinidae), the latter a parasite of the common earwig, *Forficula auricularia* L. "A few cases of hyperparasitism were noted, i.e. pupae of *Rh. antiqua* parasitized by *Dibrachys antiqua* Walker (Pteromalidae)." Identification attributed to Dr. O. Bakkendorf.
Known distribution: Denmark.

(14) *D. zelleri* (Ratzeburg). Only recent reference seen: Martelli and Arru (1957-58: 30). Identification attributed to Prof. L. Masi. Host: *Malacosoma neustrium* L.
Distribution: Italy (Sardinia).

Helocasis Wallace. One species, *H. burksi* Wallace.
Biology: Unknown.
Known distribution: North America (Pennsylvania and Illinois).

Kranophorus Graham. Seven species, five of which occur in North America, two in Europe. The genus has long been known as *Coelopisthia* (Ashmead and auctt. nec Forster). See Graham: (1956: 257, and 1969: 819).

(1) *K. bicarinata* (Girault).
Known distribution: The holotype is recorded from "North America."
(2) *K. extentus* (Walker).
Known distribution: Europe.
(3) *K. forbesii* (D.T.)
Known distribution: North America.
(4) *K. fumosipennis* (Gahan).
Known distribution: North America (Maryland).
(5) *K. intermedia* (Girault).
Known distribution: North America (Washington, D.C.)
(6) *K. pachycera* (Masi).
Known distribution: Europe.
(7) *K. suborbicularis* (Provancher).
Known distribution: North America.

Muscidifurax Girault and Saunders. Five species, of which four have been recently described by Kogan and Legner (1970). In this very comprehensive work, a key to the species is provided.

(1) *M. raptor* Girault and Saunders.
Known distribution: has been considered as practically cosmopolitan, but studies of Palearctic and Indo-Australian populations are probably necessary.
(2) *M. raptorellus* K. & L.
Known distribution: Chile, Uruguay.
(3) *M. raptoroides* K. & L.
Known distribution: Costa Rica, Mexico.
(4) *M. uniraptor* K. & L.
Known distribution: Puerto Rico.
(5) *M. zaraptor* K. & L.
Known distribution: Western U. S. (California, Utah, Arizona, New Mexico).

Nasonia Ashmead. One species, *Nasonia vitripennis* (Walker).
Known distribution: cosmopolitan.

Platneptis Bouček. One species, *Platneptis laeta* (Walker).
Known distribution: Europe.

Pseudomicromelus Gahan and Fagan. Three species.
(1) *P. australia* (Girault)
Host: Reared from larvae of *Carpocapsa pomonella.*
Known distribution: Glen Innes, New South Wales.
(2) *P. cyrene* (Walker).
Known distribution: St. John's Bluff, Fla.
(3) *P. silanus* (Walker)
Known distribution: Mount Wellington, Tasmania. European occurrence has been cited, but Graham (1969: 797) has stated his belief that the European record of *P. silanus* is probably a mistake for *Cyclogastrella deplanatus* (Nees).

Schizonotus Ratzeburg. Eight (?) species.
(1) *S. latus* (Walker)
Known distribution: North America, Europe, North Africa?
(2) *S. rotundiventris* (Girault)
Known distribution: Virginia, New Jersey, (Weiss, 1917, reported the species from Irvington, New Jersey—bred from pupa of *Plagiodera versicolor*). *S. rotundiventris* (Grlt.) may prove to be *S. latus* (Walker).
(3) *S. sieboldi* Ratzeburg.
Known distribution: Europe.

The following are of doubtful standing. I know of no confirmation of the generic placement of these Australian species. The locality of Wynnum is in the present-day limits of the city of Brisbane.

(4) *S. amabilis* Girault and Dodd.
Known distribution: Australia (Gordonvale, Cairns, Queensland).
(5) *S. arboris* Girault.
Known distribution: Australia (Wynnum).
(6) *S. doddi* Girault.
Known distribution: Australia (Gordonvale, Cairns, Queensland).
(7) *S. punctatifascies* Girault. (*Schizonotus punctifacies* Boucek, 1958,—misspelling).
Known distribution: Australia (Wynnum).
(8) *S. punctatiscutum* Girault.
Known distribution: Australia (Wynnum).

Stichocrepis Förster. One species, *S. armata* Förster.
Known distribution: Central and Eastern Europe.

Systellogaster Gahan. Two species.
(1) *S. ovivora* Gahan.
Known distribution: North America.
(2) *S. gahani* Wallace
Known distribution: North America (Missouri and Illinois).

Tritneptis Girault. Seven species, possibly all occurring in North America. Keys to various species have been presented to Gahan (1938), Graham (1969), and Burks (1971). Burks' key covers all described species except *lophyrorum.*
(1) *T. diprionis* Gahan.
Known distribution: North America, Europe.
(2) *T. doris* Burks, 1971. Host reared from pupae of *Coloradia doris* Barnes, and *Hemileuca* sp. (Lepidoptera: Saturniidae).
(3) *T. hemerocampae* Girault.
Known distribution: North America.
(4) *T. klugii* (Ratzeburg).

Known distribution: North America, Europe. (Possibly some records may refer to *lophyrorum*.)

(5) *T. koebeli* Gahan.

Known distribution: Western U. S. (California).

(6) *T. lophyrorum* (Ruschka).

Known distribution: Europe. Graham (1969: 803) states "Sweden, Germany, Czechoslovakia, USSR, Canada, U.S.A.".

(7) *T. scutellata* (Muesebeck).

Known distribution: North America.

REFERENCES CITED

ASHMEAD, W. H.

1904. Classification of the Chalcid Flies or the Superfamily Chalcidoidea, with descriptions of new species in the Carnegie Museum, collected in South America by Herbert H. Smith. Mem. Carnegie Mus. 1(4): i-xi, 225-551, 39 pls.

BOUČEK, Z.

1958. To the taxonomy of the European species of *Schizonotus* and *Caenocrepsis*—parasites of economic importance—with notes and some synonymy in Pteromalidae and Eurytomidae (Hym.). Sb. ent. Odd. nar. Mus. Praze 32: 395-404, 5 figs.

1965. A review of the chalcidoid fauna of the Moldavian SSR, with descriptions of new species (Hymenoptera). Sb. faun. Praci. ent. Odd. nar. Mus. Praze 11: 5-37.

BURKS, B. D.

1971. A new *Tritneptis*, with a revised key to the Nearctic species of the genus (Hymenoptera: Pteromalidae). Proc. Biol. Soc. Washington 84(1): pp. 1-6, figs. 1-5.

BURKS, B. D. IN KROMBEIN, K. V.

1958. Hymenoptera of America North of Mexico. Synoptic Catalog. Agr. Monogr. 2, first supplement. 305 pp.

1967. Hymenoptera of America North of Mexico. Synoptic Catalog. Agr. Monogr. 2, second supplement. 584 pp.

GAHAN, A. B.

1938. Notes on some genera and species of Chalcidoidea (Hymenoptera). Proc. Ent. Soc. Washington 40: 209-227.

GIRAULT, A. A.

1915. Australian Hymenoptera Chalciodoidea IX. The family Cleonymidae with descriptions of new genera and species. Mem. Queensland Mus. 4: 203-238.

1916. Descriptions of miscellaneous chalcid-flies. Insecutor Inscitiae Menstruus, 4: 109-121.

1917. New Australian chalcid-flies. *ibid.*, 5: 133-155.

1922. New chalcid-flies from eastern Australia. *ibid.*, 10: 148-154.

GRAHAM, M. W. R. DE V.

1956. A revision of the Walker types of Pteromalidae (Hym., Chalcidoidea). Part 2 (including descriptions of new genera and species). Ent. Monthly Mag. 92: 246-263, 6 figs.

1969. The Pteromalidae of North-western Europe. Bul. Brit. Mus. (Nat. Hist.) Entomology, Suppl. 16: 980 pp., 686 figs.

HOBBS, G. A.

1968. Controlling insect enemies of the Alfalfa Leaf-cutter Bee, *Megachile rotundata*. Canadian Ent. 100: 781-784.

KOGAN, M. AND E. F. LEGNER

1970. A biosystematic revision of the genus *Muscidifurax* (Hymenoptera: Pteromalidae) with descriptions of four new species. Canadian Ent. 102: 1268-1290, 17 figs., 1 table.

KURDJUMOV, N. V.

1913. Notes on Pteromalidae (Hymenoptera, Chalcidodea). Russk. Ent. Obozr. 13: 1-24.

MARTELLI, M. AND G. M. ARRU

1957-58. Ricerche preliminari sull 'entomofauna della Quercia da sughero ("Quercus suber" L.) in Sardegna. Boll. Zoolog. agrar. e Bachicolt. serie 2, vol. 1: 5-49.

NIELSEN, B. O.

1965. Parasitterne hos den almindelige ørentvist *(Forficula auricularia* L.). Flora og Fauna 71(2): 37-59, 8 figs., 3 tables.

NIKOL'SKAYA, M. N.

1963. The chalcid fauna of the USSR (Chalcidoidea) [English translation from Russian by A. Birron, and Cole, Z. S.]. Israel Program for Scientific Translations. Jerusalem. (Original appeared in 1952).

PECK, O.

1963. A catalogue of the Nearctic Chalcidoidea (Insecta: Hymenoptera). Canadian Ent. Suppl. 30: 1092 pp.

1969. Chalcidoid (Hymenoptera) parasites of the Alfalfa Leaf-cutter Bee, *Megachile rotundata,* in Canada. Canadian Ent. 101: 418-422.

PECK, O. *in* MUESEBECK, C. F. W., K. V. KROMBEIN, AND H. K. TOWNES

1951. Hymenoptera of America North of Mexico. Synoptic Catalog. Agr. Monogr. 2: 1420 pp.

PECK, O., Z. BOUCEK, AND A. HOFFER

1964. Keys to the Chalcidoidea of Czechoslovakia (Insecta: Hymenoptera). Mem. Ent. Soc. Canada 34: 120 pp., 289 figs.

VIGGIANI, G.

1968. Ricerche sugli Hymenoptera Chalcidoidea XVI. Su alcuni Pteromalidi nuovi per l'entomofauna italiani, con interessanti reperti biologici relativi a specie del genere *Dibrachys* Foerster. Bol. Soc. Ent. Ital. 98: 112-115, 6 figs.

WEISS, H. B.

1917. Additions to insects of New Jersey, No. 5. Ent. News 28: 214-221.

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A NEW SPECIES OF MONTANE *ANOLIS* (SAURIA, IGUANIDAE) FROM HISPANIOLA

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The West Indian island of Hispaniola is becoming increasingly well known as a center of diversity of the iguanid lizards of the genus *Anolis*. It is curious that this diversity had long gone unrecognized. Williams and Rand (1969:10) noted that seven new species of anoles have been named from Hispaniola since 1960. It is instructive to trace the history of new anoline discoveries on Hispaniola. Between 1837 and 1870, eight species of *Anolis (brevirostris* Bocourt, *chlorocyanus* Dumeril and Bibron, *coelestinus* Cope, *cybotes* Cope, *dominicensis* Reinhardt and Lütken, *ricordi* Duméril and Bibron, *baleatus* Cope, *semilineatus* Cope) were named. In the above list, I have made two deliberate nomenclatorial changes. First, I and others regard *dominicensis* Reinhardt and Lütken as subspecies of the Bahamian *A. distichus* Cope, 1861. The subspecies *dominicensis* was the first-named of several Hispaniolan subspecies (Schwartz, 1968), and for the sake of consistency, I have used the name *dominicensis* in the present context to emphasize my temporal point of view. The 1861 date for *distichus* would have done equally as well. Secondly, I regard *baleatus* as a species distinct from *ricordi*. Rationale for this division is to be found in Schwartz *(in press).* These species are either abundant and widespread in the Hispaniolan lowlands, conspicuous and almost always of moderate-to-large size (exception—*semilineatus),* or readily encountered around buildings. Thus, one might expect to encounter these lizards on a casual visit to Hispaniola.

In the period between 1919 and 1939 there was a resurgence of interest in Hispaniolan field work, with subsequent anole descriptions. The result was the naming of nine species of *Anolis (aliniger* Mertens, *altavelensis* Noble and Hassler, *longitibialis* Noble, *darlingtoni* Cochran,

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etheridgei Williams, *hendersoni* Cochran, *monticola* Shreve, *olssoni* Schmidt, *shrevei* Cochran). This list requires two comments. Although *longitibialis* is usually considered a subspecies of *cybotes,* I have taken the two taxa syntopically on the Peninsula de Barahona and have no doubt that they are specifically distinct. The name *etheridgei* Williams, 1962, is antedated by *darlingtoni* Cochran, 1939. The Cochran name had to be replaced by Williams because of potential homonymy by Etheridge's inclusion of *Xiphocercus darlingtoni* Cochran, 1935, in *Anolis.* Thus, although the name *etheridgei* was not proposed within the time span here under discussion, the species was recognized as new and named within the 1919-1939 period. It is probably not coincidental that the terminal date for this series of names just precedes the appearance of Cochran's *Herpetology of Hispaniola* (1941), and that 21 years were to pass before Hispaniola once more became an area of herpetological interest. The species of this second list show an interesting difference in trend. One species is from an offshore islet that has been, and still is, very difficult of access *(altavelensis* from Isla Alto Velo). Another is from a more accessible, but still fairly remote island *(longitibialis* from Isla Beata). Six species are montane lizards primarily or exclusively from the Cordillera Central in the Dominican Republic *(aliniger, etheridgei, shrevei)* or the southern Haitian massifs *(hendersoni, monticola, darlingtoni).* Only one *(olssoni)* is a lowland species widespread in xeric areas. Of this entire second series, none is rare (I have had no personal field experience with *altavelensis* or *monticola).* But obviously it must have required more careful planning and greater energy to reach the less accessible regions where this second group of lizards was discovered—the generally upland or Hispaniolan satellite island distributions. With two exceptions *(hendersoni, olssoni)* these are not lizards that one might casually encounter on a brief or unspecialized visit to Hispaniola.

A second resurgence of interest in Hispaniolan anoles has been occurring since 1960, under the direct influence of Ernest E. Williams at Harvard University. Pursuing this interest, he and his students have been extremely active on the island, and their discoveries have increased our knowledge of the diversity of Hispaniolan *Anolis.* Between 1960 and 1969, eight new species were named *(christophei* Williams, *cochranae* Williams, *insolitus* Williams and Rand, *koopmani* Rand, *barahonae* Williams, *rimarum* Thomas and Schwartz, *singularis* Williams, *whitemani* Williams). Of these eight species, *barahonae* was named as a subspecies of *ricordi,* but I now consider it as a distinct species (Schwartz, *in press).* Most of this third group of anoles is restricted to montane habitats *(christophei, insolitus, koopmani, rimarum). Anolis whitemani* is a lowland lizard of xeric habitats. None of these species is rare, although their ranges may be restricted *(koopmani, rimarum).*

Examination of the three lists of anoles, in historical perspective, shows that the earliest named species were conspicuous and widespread. With increased ability of collectors to reach remote regions (primarily satellite islands or high mountian ranges), the number of upland species, often with either restricted ecological requirements or geographical distribution, has increased. There is nothing striking in this gradual change in the past century-and-a-quarter. It reflects increased mobility of collectors and increased interest in the Antillean uplands. These are the areas where new taxa are most likely to be encountered, since they had either been ignored previously or were simply inaccessible.

Generally speaking, there is remarkable similarity between the temporal situation for Hispaniola and the history of *Anolis* discovery on each of the other three Greater Antillean islands. Cuban *Anolis* number 29 species, of which 15 were named between 1820 and 1870, 10 between 1916 and 1939, but only four between 1960 and 1972. Jamaica has seven species, of which six were named between 1820 and 1899, and only one between 1959 and the present. Finally, Puerto Rico has nine species, of which five were named between 1837 and 1876, three between 1904 and 1939, and one between 1960 and the present. The number of species of *Anolis* on the three islands differs greatly. The largest island, Cuba, has 29 species; Hispaniola, second largest in size, has 25; Jamaica, the third largest, has seven; and Puerto Rico, the smallest, has nine. One strong trend shown by Cuba, Jamaica, and Puerto Rico is that the majority of species descriptions falls in the early period of the nineteenth century, and that numbers of species named since then have steadily declined. In addition, early-named taxa include some with restricted distributions (*cyanopleurus* Cope and *spectrum* Gundlach and Peters, in Cuba), and some with specialized habits (*vermiculatus* Duméril and Bibron, in Cuba). The group of species on the other Greater Antilles that were named during the early portion of the present century likewise shows a gradual shift to upland forms (*clivicola* Barbour and Shreve, in Cuba; *evermanni* Stejneger, in Puerto Rico) and to forms with limited distributions (*poncensis* Stejneger and *cooki* Grant, in Puerto Rico; *ahli* Barbour, *bartschi* Cochran, *quadriocellifer* Barbour and Ramsden, *mestrei* Barbour and Ramsden, and *noblei* Barbour and Shreve, in Cuba).

Two conclusions may be reached: (1) Hispaniolan herpetological explorations have lagged behind those of the other Greater Antillean islands; (2) with the passage of time, new species of *Anolis* discovered in the Greater Antilles tend either to live in upland areas or have limited geographic distributions. It follows that Cuba, which is much larger in area than Hispaniola (114,500 versus 77,000 km^2) but paleogeographically and structurally a much more simple island than Hispaniola, probably has several undiscovered species of *Anolis* in its largely unexplored upland areas (primarily the Sierra Maestra, and other less well-known montane massifs in eastern Oriente Province). The probability is lower for either Jamaica or Puerto Rico, whose herpetofaunas are now much better known than are those of the two larger islands. In addition, there is a good possibility that remote lowland areas, especially those that are ecologically distinctive or disjunct, and satellite islands and *cayerias,* may harbor further distinctive species of *Anolis.*

That the roster of Hispaniolan *Anolis* is incomplete is manifested by the collection there of two undescribed species in 1971. Both species were secured in upland areas, one in the Sierra de Baoruco and the other in the Cordillera Central. Both ranges are in the Dominican Republic, but they lie in historically quite different areas. The Sierra de Baoruco is on the south island *(sensu* Williams, 1961) and the Cordillera Central is the interior montane massif of the north island. The two species are unrelated. The Baoruco species will be treated in a separate paper, since it presents some intriguing phenomena within the primitive *darlingtoni* complex of Greater Antillean species *(darlingtoni-occultus-insolitus).* The second species, which is a quite spectacular and fairly large anole, is described herein. My work in Hispaniola has been sponsored by National Science Foundation grants G-7977 and B-023603. I had the very capable field assistance of Danny C. Fowler and Bruce R. Sheplan. The illustrations are the work of Christopher L. Lane, to whom I am very grateful. Mr. Fowler secured the first two specimens of the new species named in his honor.

Anolis fowleri, new species

HOLOTYPE: Carnegie Museum (CM) 54131, an adult male, from 18.5 km. S.E. Constanza, 5800 feet (1769 meters), La Vega Province, Dominican Republic, one of two collected October 6, 1971, by Danny C. Fowler. Original number Albert Schwartz Field Series (ASFS) V31583.

Paratypes: ASFS V31584, same data as holotype; National Museum of Natural History (USNM) 194002, same locality as holotype, October 8, 1971, D. C. Fowler; Museum of Comparative Zoology (MCZ) 125640, same locality as holotype, October 17, 1971, D. C. Fowler; ASFS V31951, USNM 194003, same locality as holotype, October 18, 1971, D. C. Fowler; ASFS V31975, 6.5 mi. (11.7 km.) N.W. La Horma, 5400 feet (1647 meters), Peravia Province, Dominican Republic, October 19, 1971, A. Schwartz.

DIAGNOSIS: A moderately large (adults to 77 mm snout-vent length), strongly sexually dichromatic species of *Anolis,* characterized by the combination of 5 or 6 rows of loreal scales, supraorbital semicircles usually in contact, usually 1 (occasionally 2) scale between the interparietal scales and the supraorbital semicircles, subocular scales and supralabial scales in broad contact, postmental scales usually 2, 6-8 small scales in contact with the rostral scale, and 4-6 enlarged canthal scales; dorsal scales small, keeled middorsally, becoming smaller and stud-like laterally, then slightly larger and smooth ventrally, the ventral scales more or less arranged in transverse rows; all large dorsal limb scales, including supradigital scales, multicarinate; tail verticillate, caudal scales unicarinate dorsally and ventrally; males apparently not capable of complete metachrosis, having a dorsal pattern of various shades of brown and green to give a mottled or camouflage effect, females with metachrosis and dorsum strikingly patterned either (1) emerald green with middorsal brown-to-tan stripe, with two (or three, the third fragmented) slightly

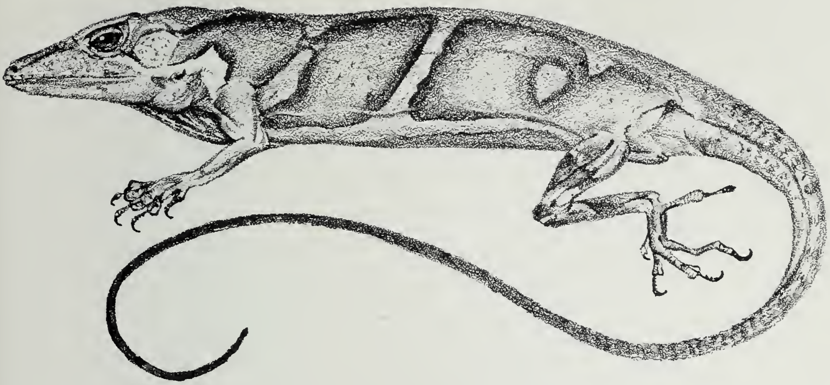

Fig. 1. Lateral view of adult female *Anolis fowleri* (ASFS V31584).

diagonal (posterior to anterior) tan stripes or bars which are connected ventrolaterally by a longitudinal brown-to-tan stripe, or (2) brown with the above pattern paler brown or tan in contrast to the dark ground color (fig. 1); juveniles patterned like females; both sexes and juveniles with a prominent pale lateronuchal blotch; dewlap brown centrally, yellow peripherally in males, rich chocolate brown in females; iris blue-green in adults.

DISTRIBUTION: The Cordillera Central in the Dominican Republic, in deciduous forest between elevations of 5400 and 5800 feet (1647 and 1769 meters).

DESCRIPTION OF HOLOTYPE: An adult male with a snout-vent length of 77 mm and tail length of 185 mm; snout scales at level of second canthal scales 7, 6 rows of loreal scales, supraorbital semicircles in contact, 1 scale on each side between the interparietal scales and the supraorbital semicircles, vertical dorsal scales in distance between tip of snout and anterior margin of orbit 24, ventrals in snout-eye distance 27, subocular scales in contact with supralabial scales, 2 postmental scales, 6 scales in posterior contact with the rostral scale, 6 and 5 enlarged canthal scales on the left and right sides of the head, respectively; subdigital lamellae on phalanges II and III of fourth toe 21. Coloration in life: dorsal ground color varying shades of brown to give a mottled or camouflage effect, the most prominent features being a dark brown occipitonuchal triangle with its apex pointed posteriorly, a yellow lateronuchal blotch which is most clearly defined (=sharp-edged) posteriorly, and indications of the lateral diagonal "female" bars in the form of a series of small grayish-tan scallops, darker-edged posteriorly; top and sides of head and upper surface of forelimbs mottled in browns, the upper surface of the hindlimbs with three broad darker brown bands (one across the knee, one on the thigh, and one on the shank); tail irregularly and inconspicuously banded and mottled with browns; entire ventral surface brown and basically continuing the dorsal pattern in a diluted fashion; dewlap brown centrally, dull yellow peripherally; iris blue-green.

VARIATION: The series consists of two adult males, one of which is the holotype and another that is somewhat damaged, two adult females, and three juvenile females. The males have snout-vent lengths of 73 and 77 mm, the females 68 and 75 mm; and the juveniles 32, 42, and 54 mm. The sexes are easily distinguished not only by the distinctive dorsal patterns in adults but also by the presence of a pair of enlarged postanal scales in males. Scutellar variation may be summarized as follows (I follow the schema used by Williams and Rand, 1969).

Head (figs. 2 & 3): Short, moderately broad posteriorly. Head scales large, papillose to rugose in males, smooth to weakly rugose in females, smallest on snout, 5 to 7 (mode 6) scales across snout at level of second canthal scale; enlarged canthals 4 to 6 (mode 5).

Nostril oval, nasal scale separated from rostral scale by two small scales. Rostral scale wide and low, 3.5 times as wide as high, in contact with 6 to 8 (mode 6) scales posteriorly.

Supraorbital semicircles large, strongly convex centrally, raised and tuberculate in males, low and smooth in females, usually in contact but separated by 1 row of smaller scales in two of six specimens. A fairly distinct row of supraciliary scales of which the anteriormost four or five are larger than the more posterior of the series, the first (=most anterior) being the largest, but not particularly elongate. Posterior and internal to the supraciliary row, about 2 to 4 irregular rows of smaller scales that blend into the enlarged scales of the supraocular disk, which has about 6 to 14 enlarged scales, the gradation between the disk scales making decisions of what is an "enlarged scale" extremely difficult. Loreal rows 5 or 6 (mode 5), regularly arranged and generally of the same rectangular shape. Temporal scales small and almost granular, but with some surface irregularities becoming almost boss-like (especially in males), about 15-18 between enlarged postocular scales and external auditory meatus. Interparietal scale lying within a deeply (in males) or moderately (in females) entrenched steep-sided depression that is confluent anteriorly with a weak frontal depression via an interocular trough, the interparietal depression bounded posteriorly by supratemporal scales that are somewhat boss-like in males, less so in females. Interparietal moderate, very much larger than the very tiny external auditory meatus which lacks a posterior entrenched area; interparietal separated from supraorbital semicircles by 1 or 2 scales (1 scale a strong mode), surrounded by relatively large scales that are papillate in males and weakly rugose in females. External auditory meatus tiny, about 6 times the size of the largest bordering temporal scale, placed ventrally but slightly above the level of the oral commissure.

Suboculars always in contact with the supralabials, anteriorly grading into the loreals, posteriorly into the temporals. Eight to 10 supralabials to center of eye.

Mental scale large, semidivided, wider than deep, in contact with 2 (modally) or 3 postmental scales; one sublabial and one infralabial in contact with mental on each side. Throat scales smallest at midthroat (transversely), becoming larger both anteriorly and posteriorly, and weakly keeled.

Trunk: Dorsal scales small, more or less granular, keeled to stud- or boss-like middorsally, becoming smaller on flanks, and somewhat larger ventrally, the ventrals smooth; no middorsal crest scales; ventrals in more or less irregular transverse rows. Vertical rows of dorsal scales 24-32 in snout-eye distance, ventral scales 23-29 in snout-eye distance.

Dewlap: Large, present in both sexes and not inset or "slotted"; dewlap scales elongate, ridged, larger than midthroat scales, more elongate than dorsal scales and larger than ventral scales; dewlap scales arranged in well-spaced longitudinal rows, the scales along the edge of the dewlap smaller and more crowded than those on the dewlap proper, and the rows on the male dewlap more widely spaced than those on the female dewlap.

Limbs and digits: Limbs long, tibial length about equal to distance between the snout and external auditory meatus. Seventeen to 21 lamellae under phalanges II and III of fourth toe. All enlarged dorsal limb scales multicarinate, including supradigital scales. Anterior thigh scales much larger than ventral scales.

Tail: Round and uncrested in both sexes, length in adults equal to about 2.5 times snout-vent length; no enlarged middorsal caudal crest scales; tail weakly verticillate dorsally, each verticil with 4-6 scales basally; caudal scales unicarinate. Scales around base of tail and behind vent smooth and slightly larger than ventral scales; no enlarged rows of ventral caudal scales.

Hemipenis: Large, bifurcate for about the distal one-third of its length, the sulcate surface smooth with the sulcus deeply entrenched, the non-sulcate surface strongly calyculate on the apical bifurcations and flounced on their basal portions; a prominent and smooth lobe at the bifurcation of the organ on the non-sulcate surface.

Coloration and pattern: As noted in the definition, *A. fowleri* is strongly sexually dichromatic. Basically, adult males are brown (and are not known to show striking metachrosis) with a camouflage pattern of various shades of browns, tans, greens, and grays.

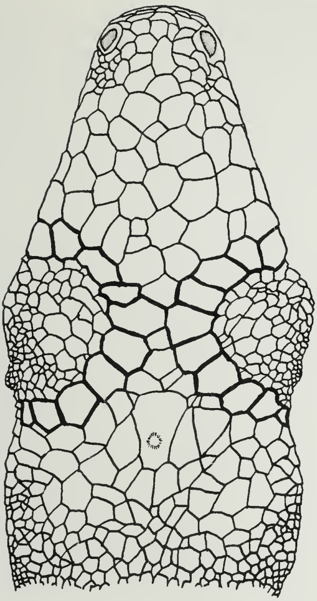

Fig. 2. Dorsal view of head of adult female *Anolis fowleri* (ASFS V31584).

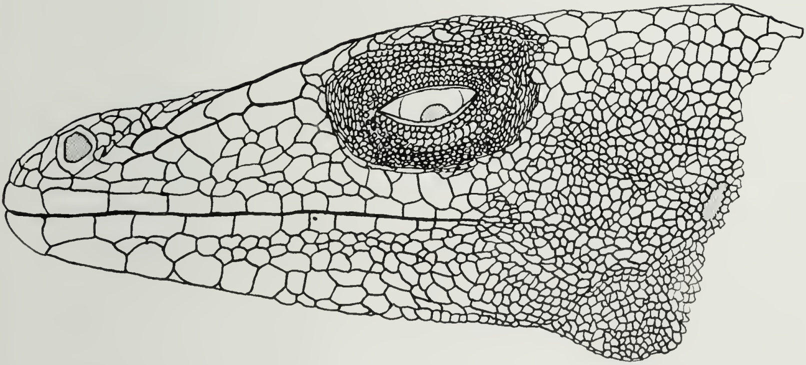

Fig. 3. Lateral view of head of adult female *Anolis fowleri* (ASFS V31584).

Adult females and juveniles (all known juveniles are females) have metachrosis and a pattern of a median dorsal stripe that sends three diagonal bars across the flanks, these bars joined ventrolaterally to each other by a ventrolateral stripe. The ground color is bright emerald green or dark brown. Since the number of specimens is few, I quote field-color notes for each in full. Those for the holotype male have already been given.

ASFS V31951 (male): Dorsal ground color green to brown with obliterative pattern of more or less irregular crossbars; a cream nuchal spot; a dark green occipitonuchal triangle; hindlimbs banded dark and pale green, the two colors separated by cream; dewlap (lizard dead) dull gray.

ASFS V31584 (female): Dorsal ground color emerald green (changing to dark brown) with a paler middorsal brown stripe and three pairs of diagonal lateral bars (the posterior pair reduced to a pair of subcircular blotches on each side in the position of the bar, the anterior pair not quite connected to the middorsal stripe), all these markings outlined with black; a yellow lateronuchal blotch; iris blue-green; dewlap rich chocolate; in dark phase, venter orange-brown, in light phase bright green, the ventral color sharply set off from the dorsal color by a ventrolateral pale (tan) stripe between the axilla and the groin; a fine pale stripe from the angle of the jaws to the yellow lateronuchal blotch; no occipitonuchal triangle present (fig. 1).

MCZ 125640 (female): Dorsal ground color bright green with a tan median dorsal stripe and narrow diagonal lateral bars on flanks; a cream lateronuchal blotch; occipitonuchal triangle present but not strikingly obvious; dewlap brown.

USNM 194003 (juvenile female—snout-vent length 54 mm): Dorsal ground color green with brown middorsal stripe and two diagonal lateral bars (third pair absent) connected ventrolaterally by a longitudinal brown stripe; lateronuchal blotch cream and a cream suborbital spot; ventral ground color green, paler than dorsum; dewlap rich chocolate.

USNM 194002 (juvenile female—snout-vent length 42 mm): Dorsal ground color bright emerald green with brown middorsal stripe, and upper surface of head with a green and contrasting occipitonuchal triangle; a white lateronuchal blotch and a white subocular spot; tail dull mottled greenish gray, limbs emerald green and gray-brown; venter pale yellow-green; dewlap dark brown.

ASFS V31975 (juvenile female—snout-vent length 32 mm): Dorsum very dark brown (almost black); head red-brown; lateronuchal blotch bright orange; a middorsal brown stripe and two pairs of diagonal brown lateral bars (third pair absent); a dark brown occipitonuchal triangle; tail pale brown basally, darker distally; venter rusty brown, brightest on throat; iris brown.

The brighter colors of the smallest juvenile and the brown iris suggest that there is ontogenetic change in basic hues from very young to adult *A. fowleri*. On the other hand, the small, brightly colored individual is from a different locality than the rest of the series, and the differences may not be ontogenetic but rather geographically correlated. Although three pairs of diagonal lateral bars seem to be the basic number, the posterior pair is often missing or reduced to remnants; and the anterior pair may be disconnected from the median dorsal stripe. Females are strikingly beautiful lizards, with brilliant green dorsum, contrasting tan-to-brown markings, at times outlined by black, and yellow-to-cream lateronuchal blotch.

COMPARISONS: *Anolis fowleri* is so striking in coloration and pattern that one is left in doubt as to what species of Hispaniolan (or indeed Antillean) anoles require comparison with it. Although males are much less strikingly colored and patterned than females, they are quite distinctive in comparison with other Hispaniolan anoles.

Richard E. Etheridge kindly offered to examine (by radiographs) specimens of *A. fowleri* in an attempt to place it in some frame of Antillean anoline reference. He stated *(in litt.,* June 9, 1972) that "*Anolis fowleri* is an *alpha* anole with autotomic caudal vertebrae, a T-shaped interclavicle, and an incriptional rib formula of 3:1. On this basis it is a member of my rather large '*carolinensis*' series. This series includes the *monticola* subseries *(christophei, etheridgei, monticola, rimarum, koopmani . . . fide* Williams)." In addition to the *monticola* subseries, the *carolinensis* series includes (on Hispaniola) *chlorocyanus, hendersoni, olssoni,* and *semilineatus,* and the Cuban species *alutaceus, argenteolus, bartschi, carolinensis, cyanopleurus, isolepis, lucius,* and *spectrum.* This list is modified and brought up-to-date nomenclatorially from Etheridge (1960:144).

The Cordillera Central in the Dominican Republic has 10 species of anoles, of which four (excluding *fowleri)* are endemic to this montane region. Non-endemic species of *Anolis* include *aliniger, chlorocyanus, christophei, cybotes, distichus,* and *baleatus.* This series includes four species *(chlorocyanus, cybotes, distichus, baleatus)* that are basically lowland species invading the mountains. None reaches an elevation of more than 6000 feet (1830 meters). Even this elevation is exceptional for these lowland species, since it is reached only at the very uppermost limit of *distichus* and *cybotes. Anolis baleatus* extends only to 4000 feet (1220 meters) and *chlorocyanus* to about the same altitude.

The four endemic species are of unusual interest. *Anolis shrevei* is restricted to very high, cool, pine-clad, windswept slopes at elevations above 6000 feet (1830 meters). *Anolis cochranae* is an elongate "grass anole" whose distribution centers in the Valle de Constanza region. This species is incompletely understood, since it may occur elsewhere outside the Cordillera Central. As presently understood, *A. cochranae* occupies suitable habitats between elevations of 1550 feet (475 meters) and about 4200 feet (1281 meters). *Anolis insolitus* is a small, primitive anole of upland deciduous forests. Its distribution lies between 3500 feet and 5800 feet (1068 and 1769 meters). Finally, *A. etheridgei* is an elongate herb-and-shrub-dwelling anole of mesic deciduous forested regions between elevations of 1800 and 6100 feet (549 and 1861 meters). *Anolis fowleri* has been taken sympatrically with *etheridgei, insolitus, cybotes,* and *distichus.* These species, along with *fowleri,* are lizards of shaded forested situations, although *distichus* and *cybotes* also occur in more open areas.

When the first pair of *A. fowleri* was collected, two characteristics were at once evident: marked sexual dichromatism, and blue-green irises. Since *A. etheridgei* is sympatric with *fowleri* and far more common (although occupying a quite different niche), I was at once struck by similarities between the two. The blue iris of *A. etheridgei* is very striking in life, as is that of *fowleri.* Secondly, *A. etheridgei* is sexually dichromatic (Thomas and Schwartz, 1967:10). Males in this species are transversely crossbanded, whereas females have a middorsal bronzy zone but without any diagonal lateral bars. Such striking sexual dichromatism is unusual in Hispaniolan (or indeed Greater Antillean) anoles. Some species of Antillean anoles have brighter colors in males than in females *(A. allisoni* on Cuba is an example), and many species have the females differently patterned, usually with a dorsal series of rhombs or diamonds in contrast to a more lineate or unpatterned dorsum in males *(A. cybotes, sagrei, shrevei,* and many other species). In the latter group, however, there is strong sexual dimorphism in size, with females much smaller than males. Only four Greater Antillean species in addition to *fowleri* and *etheridgei* are sexually dichromatic with a dorsal stripe and with both sexes about the same size. These are *hendersoni* and *rimarum* (weakly dichromatic) in Hispaniola, and *clivicola* and possibly *cyanopleurus* in Cuba. I question the situation in *cyanopleurus* since what has been interpreted as dichromatism in that species may be explained by the fact that *cyanopleurus auct.* is composed of two species.

I have presented these data in an effort to narrow the possible relatives of *fowleri.* Although *fowleri* is a large anole, its affinities with other large Hispaniolan species *(coelestinus, chlorocyanus, ricordi, baleatus, barahonae)* seem very remote. Karyotypic and electrophoretic evidence may well prove me incorrect, but for the moment I can offer nothing better on the available evidence than that *fowleri* is a member of the *monticola* complex, possibly most closely related to *etheridgei,* with which it is sympatric. I readily admit that the evidence is slim and that the presence of a well-developed dewlap in both sexes is unusual for the *monticola* series.

REMARKS: *Anolis fowleri* is associated with upland deciduous forest. The elevation at the two known localities is 1647 and 1769 meters, but I have a sight record for a lizard in a forested situation at 1586 meters.

The road between Constanza, which lies in the Cordillera Central uplands at an elevation of 1251 meters, travels southeast to San José de Ocoa at an elevation of 475 meters at the foot of the Central. Along this 87-kilometer transect of the range, the road crosses a low ridge just southeast of Constanza, then ascends the main ridge of the Cordillera to an elevation of 2379 meters in the Valle Nuevo-Alto Bandera-La Nevera area, and then once more descends to 1068 meters at the village of La Horma on the Río Ocoa. South of La Horma, the road once more ascends a relatively low ridge and then descends to San José de Ocoa. The vegetational aspect of about the first 20 kilometers southeast of Constanza is especially bleak. Slopes are generally bare, either from cultivation or naturally, with scattered pines and little or no herb or shrub understory, and are well drained by small tributary creeks and streams that are deeply entrenched in steep-sided ravines. The road approximately parallels, but for the most part lies high above, the Río Grande, and crosses that river at one point. The vegetation of the ravines is quite different from that of the adjacent open slopes. The ravines have restricted and often fairly dense stands of hardwood gallery forest. As the road begins its ascent of the main ridge of the Cordillera Central there are increasingly large areas of hardwood forest, usually still associated with streams and ravines. At an elevation of 2196 meters the vegetational picture has changed completely. The open and barren lower pine forests and ravine deciduous woods give way to extensive stands of pines with a dense understory of bracken and other herbs and shrubs, and to small, low-banked streams with very limited deciduous shrubby growth along their margins. This upland floral picture continues across the higher elevations of the mountains until the road begins to descend to La Horma where once more it enters areas of open pine forest, barren slopes, and ravine hardwoods.

As one ascends the main ridge of the Cordillera Central after crossing the Río Grande, gradually the open slopes give way to patches of hardwoods. At one such place (the type-locality) there is a small stream that has partially eroded the roadway, which here is precariously cut into the steep montane slope. The stream is under dense forest cover on the inner side of the road, and the forest ascends the mountainside between two of the road's switchbacks. We had been accustomed in previous years to visit with a Dominican family at this locality and to ask its members to collect for us. During the winter of 1970 we encountered *Anolis insolitus* at this locality, the second for that species. Collecting is limited to walking along the edge of the road and ascending the stream along a very short path constructed by the family for securing water. On the night of October 6, 1971, we sought more specimens of *A. insolitus*. This small species sleeps at night on exposed branches and twigs and, because of its pale color, is easily seen. During the evening's collecting, Fowler secured the first two specimens of *A. fowleri*. Both were adults found sleeping on tree branches of small diameter along the edge of the road and the adjacent swampy area formed here by a small spring.

Of the other *A. fowleri* obtained at the type-locality, a juvenile female (snout-vent length 42 mm.) was taken by Fowler as it was sleeping across the branches of a shrub, 8 feet (2.4 meters) above the ground, at the edge of the roadside swamp adjacent to the forest on the rising slope above. An adult female was taken by Fowler while it slept 6 feet (1.8 meters) above ground on a dead limb suspended from a vine within the edge of the forest. An adult male was encountered by Fowler and Sheplan while it slept on the vertical stem of a shrub, and a juvenile female (snout-vent length 54 mm.) was found the same night draped across the leaves of a shrub—both at the edge of the forest adjacent to the swampy area.

It seemed logical to assume that *A. fowleri* was a canopy anole and that we were sampling marginal habitats along the roadway. Accordingly, we asked the members of the family to chop a path for us up the slope through the hardwood forest. This was done, and we visited and walked this newly made path during the day and at night, but to no avail. Although the forest is dense, the evidence against *A. fowleri* being a canopy anole is negative at best. We could easily have overlooked individuals high in the canopy, since the green coloration of females blends very well with the surrounding greenery. On the other hand, all sleeping *A. fowleri* we had seen previously were readily observed.

The second locality for *A. fowleri* in some ways resembles the type-locality, but in others is remarkably different. The locality northwest of La Horma is a broadly open ravine with a creek, but lacking deciduous woods. The slopes well above the ravine are wooded, but the single juvenile taken here (snout-vent length 32 mm.) was found sleeping exposed on the top of a two-foot-high shrub in a streamside shrubby thicket. There were no trees in the immediate area. Once this juvenile was found, we searched the forest on the steep upper ravine slopes. We encountered *A. insolitus* and *A. etheridgei,* both of which are associated with *A. fowleri* at the type-locality, but we found no other specimens of the new species. The forest at the La Horma locality is somewhat more open than that at the type-locality, but it is equally mesic with ample undergrowth of vines, and trees varying from moderately high to tall.

Fowler and Sheplan saw but did not succeed in collecting what they felt certain was an adult *A. fowleri* at a locality 6.4 mi. (10.2 km.) southeast of Constanza. The situation here is much like that of the type-locality, except that the ravine woods are very narrow and the elevation lower (1586 meters). The lizard was sleeping on a diagonal dead limb with many dead leaves, about 10 feet (3.1 meters) above the ground on a sloping hillside at the edge of the ravine, where the forest gave away promptly to an open mountainside. They saw only the venter of the lizard, and when it was shot, it fell into the leaf litter and was lost.

In summary, *Anolis fowleri* appears to be associated with upland hardwood forests and their margins, where it sleeps exposed on tree limbs and shrubs between 2 feet and 10 feet (0.6 and 3.1 meters) above the ground, either oriented along the branch or draped across the leaves.

The distribution of *A. fowleri* is surely more extensive than the region from which it is presently known. Its presence at two localities well within the interior of the Cordillera Central and at the single locality near the southern edge of that massif suggests that the species is widespread in suitable situations within these mountains. Probably *A. fowleri* also occurs in the Haitian affiliates of the Cordillera Central, primarily the Massif du Nord. If this is the case, then *A. fowleri* may also be found along the Dominico-Haitian border between Loma de Cabrera and Villa Anacaona in the Dominican Republic.

REFERENCES CITED

COCHRAN, D. M.
1941. The herpetology of Hispaniola. Bull. U. S. Natl. Mus., 177:vii + 398 pp., 12 pls., 120 figs.

ETHERIDGE, R. E.
1960. The relationships of the anoles (Reptilia: Sauria: Iguanidae); an interpretation based on skeletal morphology. Univ. Microfilms, Inc., Ann Arbor, xiii + 236 pp., 11 figs., 10 maps.

SCHWARTZ, A.
1968. Geographic variation in *Anolis distichus* Cope (Lacertilia, Iguanidae) in the Bahama Islands and Hispaniola. Bull. Mus. Comp. Zool., 137(2):255-309, 4 figs., 2 pls.
[In press]. An analysis of variation in the Hispaniolan giant anole, *Anolis ricordi* Duméril and Bibron.

THOMAS, R., AND A. SCHWARTZ.
1967. The monticola group of the lizard genus *Anolis* in Hispaniola. Breviora, Mus. Comp. Zool., 261:1-27, 14 figs., 1 pl.

WILLIAMS, ERNEST E.
1961. Notes on Hispaniolan herpetology, 3. The evolution and relationships of the *Anolis semilineatus* group. Breviora, 136:1-8.

WILLIAMS, E. E., AND A. S. RAND.
1969. *Anolis insolitus,* a new dwarf anole of zoogeographic importance from the mountains of the Dominican Republic. Breviora, Mus. Comp. Zool., 326:1-21, 6 figs.

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